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Competitive Interactions and Resource Partitioning Between Northern Spotted Owls and Barred Owls in Western Oregon

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ABSTRACT The federally threatened northern spotted owl (*Strix occidentalis caurina*) is the focus of intensive conservation efforts that have led to much forested land being reserved as habitat for the owl and associated wildlife species throughout the Pacific Northwest of the United States. Recently, however, a relatively new threat to spotted owls has emerged in the form of an invasive competitor: the congeneric barred owl (*S. varia*). As barred owls have rapidly expanded their populations into the entire range of the northern spotted owl, mounting evidence indicates that they are displacing, hybridizing with, and even killing spotted owls. The range expansion by barred owls into western North America has made an already complex conservation issue even more contentious, and a lack of information on the ecological relationships between the 2 species has hampered recovery efforts for northern spotted owls. We investigated spatial relationships, habitat use, diets, survival, and reproduction of sympatric spotted owls and barred owls in western Oregon, USA, during 2007–2009. Our overall objective was to determine the potential for and possible consequences of competition for space, habitat, and food between these previously allopatric owl species. Our study included 29 spotted owls and 28 barred owls that were radio-marked in 36 neighboring territories and monitored over a 24-month period. Based on repeated surveys of both species, the number of territories occupied by pairs of barred owls in the 745-km² study area (82) greatly outnumbered those occupied by pairs of spotted owls (15). Estimates of mean size of home ranges and core-use areas of spotted owls (1,843 ha and 305 ha, respectively) were 2–4 times larger than those of barred owls (581 ha and 188 ha, respectively). Individual spotted and barred owls in adjacent territories often had overlapping home ranges, but interspecific space sharing was largely restricted to broader foraging areas in the home range with minimal spatial overlap among core-use areas. We used an information-theoretic approach to rank discrete-choice models representing alternative hypotheses about the influence of forest conditions, topography, and interspecific interactions on species-specific patterns of nighttime resource selection. Spotted owls spent a disproportionate amount of time foraging on steep slopes in ravines dominated by old (>120 yr) conifer trees. Barred owls used available forest types more evenly than spotted owls, and were most strongly associated with patches of large hardwood and conifer trees that occupied relatively flat areas along streams. Spotted and barred owls differed in the relative use of old conifer forest (greater for spotted owls) and slope conditions (steeper slopes for spotted owls), but we found no evidence that the 2 species differed in their use of young, mature, and riparian-hardwood forest types. Mean overlap in proportional use of different forest types between individual spotted owls and barred owls in adjacent territories was 81% (range = 30–99%). The best model of habitat use for spotted owls indicated that the relative probability of a location being used was substantially reduced if the location was within or in close proximity to a core-use area of a barred owl. We used pellet analysis and measures of food-niche overlap to determine the potential for dietary competition between spatially associated pairs of spotted owls and barred owls. We identified 1,223 prey items from 15 territories occupied by spotted owls and 4,299 prey items from 24 territories occupied by barred owls. Diets of both species were dominated by nocturnal mammals, but diets of barred owls included many terrestrial, aquatic, and diurnal prey species that were rare or absent in diets of spotted owls. Northern flying squirrels (*Glaucomys sabrinus*), woodrats (*Neotoma fuscipes*, *N. cinerea*), and lagomorphs (*Lepus americanus*, *Sylvilagus bachmani*) were primary prey for both owl species, accounting for 81% and 49% of total dietary biomass for spotted owls and barred owls, respectively. Mean dietary overlap between pairs of spotted and barred owls in adjacent territories was moderate (42%; range = 28–70%). Barred owls displayed demographic superiority over spotted owls; annual survival probability of spotted owls from known-fate analyses (0.81, SE = 0.05) was lower than that of barred owls (0.92, SE = 0.04), and pairs of barred owls produced an average of 4.4 times more young than pairs of spotted owls over a 3-year period. We found a strong, positive relationship between seasonal (6-month) survival probabilities of both species and the

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proportion of old (>120 yr) conifer forest within individual home ranges, which suggested that availability of old forest was a potential limiting factor in the competitive relationship between these 2 species. The annual number of young produced by spotted owls increased linearly with increasing distance from a territory center of a pair of barred owls, and all spotted owls that attempted to nest within 1.5 km of a nest used by barred owls failed to successfully produce young. We identified strong associations between the presence of barred owls and the behavior and fitness potential of spotted owls, as shown by changes in movements, habitat use, and reproductive output of spotted owls exposed to different levels of spatial overlap with territorial barred owls. When viewed collectively, our results support the hypothesis that interference competition with barred owls for territorial space can constrain the availability of critical resources required for successful recruitment and reproduction of spotted owls. Availability of old forests and associated prey species appeared to be the most strongly limiting factors in the competitive relationship between these species, indicating that further loss of these conditions can lead to increases in competitive pressure. Our findings have broad implications for the conservation of spotted owls, as they suggest that spatial heterogeneity in vital rates may not arise solely because of differences among territories in the quality or abundance of forest habitat, but also because of the spatial distribution of a newly established competitor. Experimental removal of barred owls could be used to test this hypothesis and determine whether localized control of barred owl numbers is an ecologically practical and socio-politically acceptable management tool to consider in conservation strategies for spotted owls. © 2014 The Wildlife Society

KEY WORDS barred owl, competition, home range, niche overlap, northern spotted owl, reproduction, resource partitioning, *Strix occidentalis caurina*, *Strix varia*, survival.

Interacciones Competitivas y Repartición de Recursos Entre *S. occidentalis caurina* y *Strix varia* en el Oeste de Oregon

RESUMEN *S. occidentalis caurina* es una especie amenazada y constituye el eje de intensos esfuerzos de conservación que han permitido la protección de bosques como hábitat de la especie y la protección de otras especies de vida silvestre en el Pacífico Noroccidental de los Estados Unidos. Recientemente, sin embargo, una nueva amenaza para *S. occidentalis caurina* ha emergido en la forma de un competidor invasivo: su congénere *S. varia*. A medida que *S. varia* ha expandido rápidamente sus poblaciones dentro del rango entero de distribución de *S. occidentalis caurina*, más evidencia indica que *S. varia* está desplazando, matando e incluso se está hibridizando con *S. occidentalis caurina*. El rango de expansión de *S. varia* en el occidente de Norte América ha hecho que un problema de conservación complejo sea aún más polémico, y la carencia de información sobre las relaciones ecológicas entre las dos especies ha obstaculizado los esfuerzos de recuperación de *S. occidentalis caurina*. Investigamos las relaciones espaciales, el uso de hábitat, la dieta, la supervivencia y la reproducción de *S. occidentalis caurina* y *S. varia* en condiciones de simpatria en el occidente de Oregon, USA, durante 2007–2009. Nuestro objetivo general fue determinar el potencial y posibles consecuencias de la competencia por espacio, hábitat, y dieta entre estas especies previamente alopátricas. Nuestro estudio incluyó 29 individuos de *S. occidentalis caurina* y 28 individuos de *S. varia* que fueron radio- marcados en 36 territorios vecinos y monitoreados por un periodo de más de 24 meses. Con base en muestreos repetidos de ambas especies, en el área de estudio correspondiente a 745-km², el número de territorios ocupados por parejas de *S. varia* (82) superó en gran medida el número de territorios ocupados por parejas de *S. occidentalis caurina* (15). El tamaño medio estimado de rangos de hogar y áreas de uso básico de *S. occidentalis caurina* fue 1,843 ha y 305 ha respectivamente, 2–4 veces más extenso que el promedio estimado para *S. varia* (581 ha y 188 ha, respectivamente). Individuos de ambas especies en territorios adjuntos tienen a menudo rangos de hogar superpuestos pero el espacio inter-específico compartido estuvo ampliamente restringido a extensas áreas de forrajeo en el rango de hogar con una superposición espacial mínima entre las áreas de uso básico. Usamos un enfoque de la información teórica para categorizar los modelos de escogencia discreta que representan las hipótesis alternativas sobre la influencia de las condiciones del bosque, la topografía, y las relaciones interespecíficas de patrones específicos de las especies en la selección nocturna de recursos. *S. occidentalis caurina* usaron una desproporcionada cantidad de tiempo forrajeando en pendientes abruptas en barrancos dominados por coníferas de más de 120 años. *S. varia* usaron los diferentes tipos de bosque de manera más equitativa que *S. occidentalis caurina*, y estuvieron fuertemente asociados con parches de árboles de madera dura y coníferas que ocuparon relativamente áreas planas a lo largo de corrientes de agua. *S. occidentalis caurina* y *S. varia* se diferenciaron en el uso relativo de bosques viejos de coníferas (mucho más grande para *S. occidentalis caurina*) y las condiciones de pendiente (pendientes más pronunciadas para *S. occidentalis caurina*), pero no encontramos evidencia que ambas especies se diferencien en el uso de bosques jóvenes, maduros y tipo de bosques riparios de madera dura. La superposición media en el uso proporcional de diferentes tipos de bosques entre individuos de *S. occidentalis caurina* y *S. varia* en territorios adyacentes fue 81% (rango = 30–99%). El mejor modelo de uso de hábitat para *S. occidentalis caurina* indicó que la probabilidad relativa de un lugar siendo usado fue reducida

substantialmente si el lugar estuvo dentro o en cercanías de una área de uso básico de *S. varia*. Usamos análisis de egagrópilas y medidas de superposición del nicho alimenticio para determinar el potencial de competencia dietario entre parejas espacialmente asociadas de *S. occidentalis caurina* y *S. varia*. Identificamos 1,223 ítems de presa en los 15 territorios ocupados por *S. occidentalis caurina* y 4,299 ítems de presa en los 24 territorios ocupados por *S. varia*. La dieta de ambas especies estuvo dominada por mamíferos nocturnos pero la dieta de *S. varia* incluyó muchos ítems terrestres, acuáticos y especies diurnas que fueron raras o ausentes en la dieta de *S. occidentalis caurina*. Entre las presas primarias de ambas especies registramos *Glaucomys sabrinus*, *Neotoma fuscipes*, *N. cinerea*, *Lepus americanus* y *Sylvilagus bachmani*, representando el 81% y el 49% de la biomasa total de la dieta para *S. occidentalis caurina* y *S. varia* respectivamente. La superposición media de la dieta entre parejas de *S. occidentalis caurina* y *S. varia* en territorios adyacentes fue moderada (42%; rango = 28–70%). *Strix varia* presentó superioridad demográfica sobre *S. occidentalis caurina*; la probabilidad de supervivencia anual de *S. occidentalis caurina* generada en análisis de supervivencia de destino conocido (0.81, SE = 0.05) fue mucho más baja que la de *S. varia* (0.92, SE = 0.04), y parejas de *S. varia* produjeron un promedio de 4.4 veces más juveniles que parejas de *S. occidentalis caurina* en un periodo de más de 3 años. Encontramos una relación positiva entre las probabilidades estacionales de supervivencia (6 meses) de ambas especies y la proporción de bosques viejos de coníferas (>120 años) dentro de rangos de hogar individuales, lo cual sugiere que la disponibilidad de bosques viejos fue un potencial factor limitante en la relación competitiva de estas dos especies. El número anual de juveniles producido por *S. occidentalis caurina* aumentó de manera linear cuando se incrementó la distancia desde el centro de un territorio de una pareja de *S. varia*, y todos los *S. occidentalis caurina* que intentaron anidar dentro de 1.5 km de un nido usado por *S. varia* no lograron producir juveniles de manera exitosa. Identificamos fuertes asociaciones entre la presencia de *S. varia* y el comportamiento y potencial éxito reproductivo de *S. occidentalis caurina*, como se mostró en los cambios de movimiento, uso de hábitat y capacidad reproductiva de esta especie expuesta a diferentes niveles de superposición espacial con individuos territoriales de *S. varia*. Visto de manera integral, nuestros resultados soportan la hipótesis que la competencia por interferencia con *S. varia* por espacio territorial puede restringir la disponibilidad de recursos críticos para el reclutamiento y reproducción exitosa de *S. occidentalis caurina*. La disponibilidad de bosques viejos y las especies de presa asociadas parecen ser los factores más limitantes en la relación de competencia entre estas especies, indicando que la pérdida posterior de estas condiciones puede producir un aumento en la presión competitiva. Nuestros hallazgos tienen amplias implicaciones para la conservación de *S. occidentalis caurina*, ya que sugieren que la heterogeneidad espacial en las tasas vitales no solamente se originan debido a las diferencias en la calidad o abundancia de hábitat boscoso entre los territorios sino que también depende de la distribución espacial de un nuevo competidor recientemente establecido. La remoción experimental de *S. varia* podría ser usada para evaluar esta hipótesis y determinar si un control localizado del número de *S. varia* es una herramienta de manejo ecológicamente práctica y sociopolíticamente aceptable como estrategia de conservación de *S. occidentalis caurina*.

Interactions Concurrentielles et Partages des Ressources Entre les Chouettes Tachetées du Nord et les Chouettes Rayées à l'Ouest de l'Oregon

RÉSUMÉ La chouette tachetée du Nord (*Strix occidentalis caurina*), menacée fédéralement est au centre d'intensifs efforts de préservation. Ces efforts ont menés à réserver beaucoup d'espaces boisés comme habitat pour la chouette et d'autres espèces associées dans le Pacifique Nord Ouest des Etats Unis. Récemment, cependant, une menace relativement nouvelle pour la chouette tachetée est apparue, sa congénère la chouette rayée (*S. varia*), un concurrent envahissant. Les chouettes rayées connaissent une rapide expansion de leur population et ont envahi le territoire de la chouette tachetée. De preuves croissantes montrent qu'elles forcent les chouettes tachetées à se déplacer, s'accouplent avec elles voire les tuent. L'expansion des chouettes rayées en Amérique du Nord a transformé ce problème de préservation déjà complexe en un sujet encore plus controversé. De plus, le manque d'information concernant les relations écologiques entre ces 2 espèces entrave les efforts de protection des chouettes tachetées. Sur la période 2007–2009, nous avons étudié les relation spatiales, l'utilisation de l'habitat, le régime alimentaire ainsi que la survie et le système de reproduction des espèces sympatriques que sont les chouettes tachetées et rayées dans l'Ouest de l'Oregon, Etats Unis. Notre objectif principal était de déterminer la potentialité et les conséquences éventuelles dans la lutte pour l'espace, l'habitat et la nourriture entre ces espèces de chouettes auparavant allopatriques. Notre étude portait sur 29 chouettes tachetées et 28 chouettes rayées suivies par radio sur 36 territoires limitrophes et observées durant une période de 24 mois. Basé sur des études répétées sur les deux espèces, le nombre de territoires occupés par des couples de chouettes rayées dans la zone d'étude de 745 km² (82) surpassaient

considérablement les territoires occupés par des couples de chouettes tachetées (15). Les estimations sur la taille moyenne de l'habitat et des secteurs clés des chouettes tachetées (respectivement 1,843 ha et 305 ha) était 2 à 4 fois plus larges que celles des chouettes rayées (respectivement 581 ha et 188 ha). Les chouettes tachetées et rayées isolées vivant sur des territoires adjacents avaient fréquemment un chevauchement de leurs espaces vitaux mais la délimitation de leur espace interspécifique se bornait en général à une aire d'alimentation plus vaste du domaine vital avec un minimum d'empiètement spatial sur les secteurs clés. Nous avons utilisé une approche théorique de l'information pour classer séparément des modèles représentant des hypothèses alternatives sur l'influence de la condition des forêts, la topographie, et les interactions interspécifiques sur les habitudes propres à chaque espèce pour la sélection des ressources nocturnes. La chouette tachetée a passé un temps disproportionné à se nourrir sur les pentes escarpées ou poussaient d'anciens conifères (plus de 120 ans). Les chouettes rayées utilisaient mieux les différents types de forêts disponibles que les chouettes tachetées, et était le plus fortement associées aux parcelles de grands feuillus et de conifères autour de zones relativement plates le long de cours d'eau. Les chouettes tachetées et rayées différaient dans leur utilisation des anciennes forêts de conifères (lieu de prédilection pour les chouettes tachetées) et la condition des pentes (pentes escarpées pour les chouettes tachetées) mais nous n'avons trouvé aucune preuve que ces 2 espèces différaient dans leur utilisation de feuillus jeunes, de forêts matures, et forêts ripicoles. En proportion, le recoupement moyen de l'utilisation des différents types de forêt entre les chouettes tachetées et rayées vivant sur des territoires adjacents était de 81% (intervalle = 30–99%). Le meilleur modèle d'utilisation de l'habitat de la chouette tachetée indiquait que la relative probabilité qu'un emplacement soit utilisé était réduit substantiellement si l'emplacement était à l'intérieur ou à proximité d'une zone couramment fréquentée par les chouettes rayées. Nous avons utilisé l'analyse des pelotes de régurgitation et les mesures de recoupement des niches alimentaires pour déterminer la potentialité de concurrence alimentaire entre les couples de chouettes tachetées et de chouettes rayées spatialement associées. Nous avons identifié 1,223 proies sur les 15 territoires occupés par des chouettes tachetées et 4,299 proies sur les 24 territoires occupés par des chouettes rayées. Le régime alimentaire des deux espèces était en grande partie composé de mammifères nocturnes mais celui des chouettes rayées comprenait beaucoup de proies terrestres, aquatiques et diurnes, proies rares ou absentes dans le régime des chouettes tachetées. Les écureuils volants du Nord (*Glaucomys sabrinus*), les rats des bois (*Neotoma fuscipes*, *N. cinerea*) et les lagomorphes (*Lepus americanus*, *Sylvilagus bachmani*) étaient des proies principales pour les deux espèces de chouettes, représentant respectivement 81% et 49% de la masse diététique des chouettes tachetées et des chouettes rayées. La moyenne de recoupement de leur régime était modéré entre les couples de chouettes tachetées et rayées sur des territoires limitrophes (42%; gamme = 28–70%). Les chouettes rayées manifestaient une supériorité démographique sur les chouettes tachetées; la probabilité annuelle de survie pour les chouettes tachetées à partir d'analyses de leur destin connu (0.81, SE = 0.05) était inférieure à celle des chouettes rayées (0.92, SE = 0.04) et sur une période de 3 ans, les couples de chouettes rayées avaient en moyenne 4.4 fois plus de descendants que les couples de chouettes tachetées. Nous avons trouvé une relation forte et positive entre la probabilité de survie saisonnière des deux espèces (6 mois) et la proportion d'anciennes forêts de conifères (≥ 120 ans) situées dans leur zones d'habitation, ce qui suggère que la disponibilité de la vieille forêt est un obstacle potentiel à la compétition entre ces 2 espèces. Le nombre de naissances annuelles chez les chouettes tachetées a suivi une croissance linéaire en lien avec l'augmentation de la distance du centre de territoire d'un couple de chouettes rayées. Toute chouette tachetée ayant tenté de nicher à 1.5 km d'un nid utilisé par des chouettes rayées n'a eu aucune progéniture. Nous avons identifié de fortes corrélations entre la présence de chouettes rayées et le comportement ainsi que le potentiel d'adaptation chez les chouettes tachetées, démontré par un changement dans leurs mouvements, dans leur utilisation de l'habitat et leur reproduction quand exposées à différents niveaux d'empiètement spatial avec les chouettes rayées territoriales. Nos résultats supportent l'hypothèse que l'interférence concurrentielle de l'espace territorial avec les chouettes rayées peut limiter la disponibilité de ressources essentielles nécessaires à la réussite du peuplement et de la reproduction de la chouette tachetée. La disponibilité de forêts anciennes et des proies qui y sont associées semble être les plus puissants facteurs limitant la relation compétitive entre ces espèces, ce qui signifie à contrario que la perte de ces conditions peut entraîner une augmentation de la pression concurrentielle. Nos résultats ont d'importantes répercussions dans la lutte pour sauver les chouettes tachetées, car ils suggèrent que l'hétérogénéité spatiale des indices vitaux ne surviennent pas seulement à cause des différences entre les territoires en terme de qualité ou d'abondance d'habitat forestier mais aussi à cause de la répartition spatiale d'un concurrent fraîchement établi. La suppression expérimentale des chouettes rayées pourrait être utilisée pour tester cette hypothèse et pour déterminer si le contrôle localisé du nombre de chouettes rayées est un outil de gestion écologiquement pratique et socialement acceptable à considérer en tant que stratégie de préservation pour les chouettes tachetées.

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INTRODUCTION

Two species cannot permanently coexist unless they are doing things differently. In his classic work on *Paramecium*, Gause (1935) proposed what later became known as the “competitive exclusion principle,” one of ecology’s few guiding principles. Inspired in part by the work of Gause and others (Volterra 1926, Lotka 1932), the study of interspecific competition and patterns of coexistence has become one of ecology’s central pursuits (MacArthur and Levins 1967, Schoener 1982, Connell 1983, Dhondt 2012). Interspecific competition has been defined as “an interaction between members of two or more species that, as a consequence of either exploitation of a shared resource or of interference related to that resource, has a negative effect on fitness-related characteristics of at least one species” (Wiens 1989:7). This definition implies that 1) a resource must be limited in supply for competition to occur, and 2) the effects of competition operate primarily at the individual level. As the effects of competition accumulate across individuals, however, they can eventually be translated to the population or metapopulation levels, leading to overall reductions in population growth rate of 1 or both species.

Competition theory further predicts that the coexistence of ecologically similar species can be maintained by niche differentiation. In a classic example, MacArthur (1958) found that 5 closely related species of *Dendroica* warblers coexisted by foraging in different portions of trees in a coniferous forest. Although the species greatly overlapped spatially, each species spent the majority of its foraging time in a unique portion of the trees. In England, Lack (1971) found that niche segregation in coexisting *Parus* tits in broad-leaved woodlands was mediated by differences in body size and the size and shape of the birds’ beaks. These slight differences in morphology translated to differences in the size of insect prey taken and the hardness of seeds used. In

contrast to these traditional examples of long-established niche differentiation, the recent invasion of an ecosystem by an alien species poses a different kind of predicament because there may not have been sufficient evolutionary time for segregation in resource use to develop. In this scenario, competitive pressure intensifies as ecologically similar species become restricted to a common set of resources, leading to reduced fecundity or survival of 1 or more species. Invasive species (also referred to as foreign or exotic) are often perceived as organisms that originate from far-away regions and are transplanted predominantly via human vectors (Valéry et al. 2009). Also common but less recognized are native invaders—species that under the influence of events such as climatic changes or human modifications to habitat have become invasive by expanding their range into new areas (Simberloff 2011, Carey et al. 2012). Native invaders can cause similar harmful ecological and economic impacts to those commonly associated with non-native or introduced invasive species, because even small shifts in relative abundance among species in a community can lead to substantial changes in resource availability and food-web dynamics (Acevedo and Cassinello 2009, Valéry et al. 2009). Native invaders can reduce or extirpate other native species by niche displacement, competition, alteration of nutrient cycles, hybridization, and introgression (Carey et al. 2012). In the Pacific Northwest of the United States, increasing evidence indicates that the recent range expansion and invasion of the barred owl (*Strix varia*) may represent this type of competitive threat to the closely related northern spotted owl (*S. occidentalis caurina*; Kelly et al. 2003, Anthony et al. 2006, Buchanan et al. 2007, Gutiérrez et al. 2007, Forsman et al. 2011).

Conservation efforts for the northern spotted owl began as early as 1973 in Oregon, but the sub-species was not listed federally as threatened until 1990 (U.S. Department of the Interior [USDI] 1990, Noon and McKelvey 1996). The original listing

was based on the owl's strong association with old conifer forest and declining trends in both old-forest habitat and owl populations (USDI 1990). The conservation and management of spotted owls has since become one of the largest and most visible wildlife conservation issues in U.S. history (Noon and Franklin 2002). Management of spotted owls has been a complicated and controversial interagency effort leading to much forested land being reserved as habitat for the owl and associated wildlife species in the Pacific Northwest of the United States (U.S. Department of Agriculture [USDA] Forest Service and USDI Bureau of Land Management 1994). Despite these efforts, populations of northern spotted owls have continued to decline throughout much of the sub-species' range (Forsman et al. 2011). The most recent meta-analysis of demographic rates of spotted owls on 11 study areas indicated that several populations in Washington and northern Oregon had declined by 40–60% between 1985 and 2008, but populations on federal lands in southern Oregon and northern California were relatively stationary or only slightly declining (Forsman et al. 2011). These authors concluded that an increasing number of barred owls and loss of habitat were at least partially responsible for these declines, especially in parts of Washington and northern Oregon where barred owls had been present the longest.

The barred owl invasion into the Pacific Northwest has been well documented, and the newly extended range of this species now completely overlaps that of the northern spotted owl (Kelly et al. 2003, Livezey 2009). Evidence suggests that barred owls outnumber spotted owls in British Columbia (Dunbar et al. 1991), the Washington Cascades (Pearson and Livezey 2003, Forsman et al. 2011), and western Oregon (Wiens et al. 2011), which are areas that were colonized sequentially by barred owls as they expanded their populations southward into the Pacific Northwest (Livezey 2009). Barred owls are similar to spotted owls both morphologically and ecologically, although barred owls are slightly larger (Gutiérrez et al. 2004, Wiens 2012), use smaller home ranges (Hamer et al. 2007, Singleton et al. 2010), have more diverse diets (Hamer et al. 2001), and use a wider range of forest conditions for nesting (Herter and Hicks 2000, Pearson and Livezey 2003, Livezey 2007). Barred owls also appear to defend their territories more aggressively than spotted owls (Van Lanen et al. 2011), which, in the most extreme cases, may result in spotted owl mortality (Leskiw and Gutiérrez 1998). When viewed collectively, the behavioral and life-history traits exhibited by barred owls may give them a significant advantage over spotted owls when competing for critical resources such as territorial space, nesting and foraging habitat, and food.

Central to any definition of interspecific competition is the requirement that interactions have a detrimental effect on the population characteristics of 1 or more species. Evidence of a negative relationship between barred owl occurrence and population characteristics of spotted owls include: 1) a decline in occupancy rates of historical spotted owl territories where barred owls were detected (Kelly et al. 2003, Olson et al. 2005, Kroll et al. 2010, Dugger et al. 2011); 2) a negative relationship between the occurrence of barred owls and apparent survival of spotted owls (Anthony et al. 2006, Forsman et al. 2011, Glenn et al. 2011a); 3) a negative relationship between the presence of

barred owls and fecundity of spotted owls (Olson et al. 2004, Forsman et al. 2011); and 4) declining rates of population change in portions of the spotted owl's range where barred owls have been present the longest (Anthony et al. 2006, Forsman et al. 2011). Despite this potential for interspecific competition, all aforementioned studies that reported a negative effect of barred owls on spotted owls were based on coarse-scale measures of barred owl occurrence from incidental detections during surveys of spotted owls. Barred owls may often go undetected in surveys of spotted owls, however (Bailey et al. 2009, Wiens et al. 2011), which weakens inferences regarding the magnitude, mechanisms, and possible outcome of competition. Moreover, it remains unclear how joint exploitation of resources or territorial displacement (or both) may actually translate to a negative effect on the demographic performance of spotted owls.

Ultimately, the conservation of the spotted owl may need to be extended from ameliorating the effects of habitat loss and fragmentation to account for the presence of a newly established competitor (Peterson and Robins 2003, Dugger et al. 2011). The challenges associated with preserving spotted owl habitat while accounting for the potentially overriding effects of a superior competitor at high densities are far-reaching and complex. The uncertainties associated with barred owls have led scientists and land managers to conclude that a better understanding of the ecological relationships between the 2 species is needed to inform future decisions regarding conservation and management of the northern spotted owl and its habitats (Buchanan et al. 2007, U.S. Fish and Wildlife Service [USFWS] 2011). Specific information on competitive interactions and partitioning of resources between the species will be particularly relevant in guiding future management decisions. Such information can help determine how proposed management actions might alleviate or exacerbate competitive interactions and inform decisions concerning recent proposals to control barred owl populations to benefit spotted owls (Buchanan et al. 2007, Gutiérrez et al. 2007, USFWS 2011).

We conducted a comprehensive investigation of the ecological relationships between sympatric northern spotted owls and barred owls in the central Coast Ranges of western Oregon, USA, during 2007–2009. The overall objective of our study was to determine the potential for and possible consequences of competition for territorial space, habitat (i.e., the collection of resources and environmental conditions present in an area that promote occupancy), and food between these ecologically similar owl species. Using a combination of population surveys and radio-telemetry methods, we addressed 2 primary questions: 1) What is the degree of resource partitioning between spotted and barred owls in an area where the 2 species co-occur? 2) Does the presence of barred owls have the potential to influence space-use, resource selection, and fitness characteristics of spotted owls? We examined these questions by directly monitoring spatial relationships, habitat use, diets, survival, and reproduction of sympatric spotted owls and barred owls. We predicted that if competition between the 2 species was occurring, then 1) spotted owls should alter the extent of space use or selection of foraging habitats with increased proximity to or incidence of nearby barred owls; 2) use of preferred foraging habitats by spotted owls should be

negatively associated with the presence of barred owls; and 3) fitness potential (i.e., survival and reproduction) of individuals should be negatively associated with increasing levels of exposure to competitors. Herein, we characterize resource use and demography of sympatric northern spotted owls and barred owls to evaluate the support for these predictions.

STUDY AREA

The 975-km² study area was located in the central Coast Ranges of western Oregon, USA (Fig. 1). This area included a mixed ownership of lands administered by the United States Bureau of Land Management (BLM; 48%), large timber companies (47%), Oregon Department of Forestry (3%), and small private landowners (2%). We selected this area based on many considerations, including existing data on locations of spotted owls, year-round access to owl sites, land ownership boundaries, and locations of ongoing demographic studies of spotted owls (where owls could not be radio-marked). Throughout the study area, 1-mile² (2.6-km²) sections of federal or state-owned lands alternated with sections of privately owned lands, which produced a checkerboard pattern of land ownership and forest structure (Richardson 1980). Divergent forest management practices among public and private ownerships had resulted in strong contrasts in forest conditions; federal and state lands contained more mature and old forests, whereas private lands managed for timber production were dominated by young (<40 yr), even-aged forests and recent clear-cuts (Stanfield et al. 2002, Spies et al. 2007). Elevation ranged from 275 m to 2,300 m, with

the terrain being highly dissected by steep slopes and a high density of streams. Forests were dominated by Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and western redcedar (*Thuja plicata*). Mixed-species stands of hardwoods, especially bigleaf maple (*Acer macrophyllum*) and red alder (*Alnus rubra*), occupied many riparian areas and recently disturbed sites. Common understory herbs and shrubs included swordfern (*Polystichum munitum*), salal (*Gaultheria shallon*), vine maple (*Acer circinatum*), and Oregon-grape (*Berberis nervosa*). Approximately 38% of the study area included a patchwork of mature (60–120 yr) or old-growth (>120 yr) conifer forest within a matrix of recent clear-cuts and young forests growing in old clear-cuts (Appendices A and B).

The study area was bounded on the north and south by 2 long-term spotted owl demographic study areas (Oregon Coast Ranges and Tyee; Forsman et al. 2011). Based on incidental detections of barred owls during annual surveys of spotted owls, Forsman et al. (2011:80) concluded that the relative abundance of barred owls in the Oregon Coast Ranges and Tyee study areas was low during the early 1990s, but that the proportion of spotted owl territories where barred owls were detected increased steadily to a high of approximately 72% in 2009. Previous mark-recapture studies of demography in our study area during 1989–1993 indicated that adult (≥ 3 yr) spotted owls had relatively high survival (0.85, SE = 0.03), the proportion of pairs nesting varied extensively among years (range = 0.12–0.81), and the population was declining ($\lambda = 0.91$, SE = 0.03; Thrailkill et al. 1996:56).

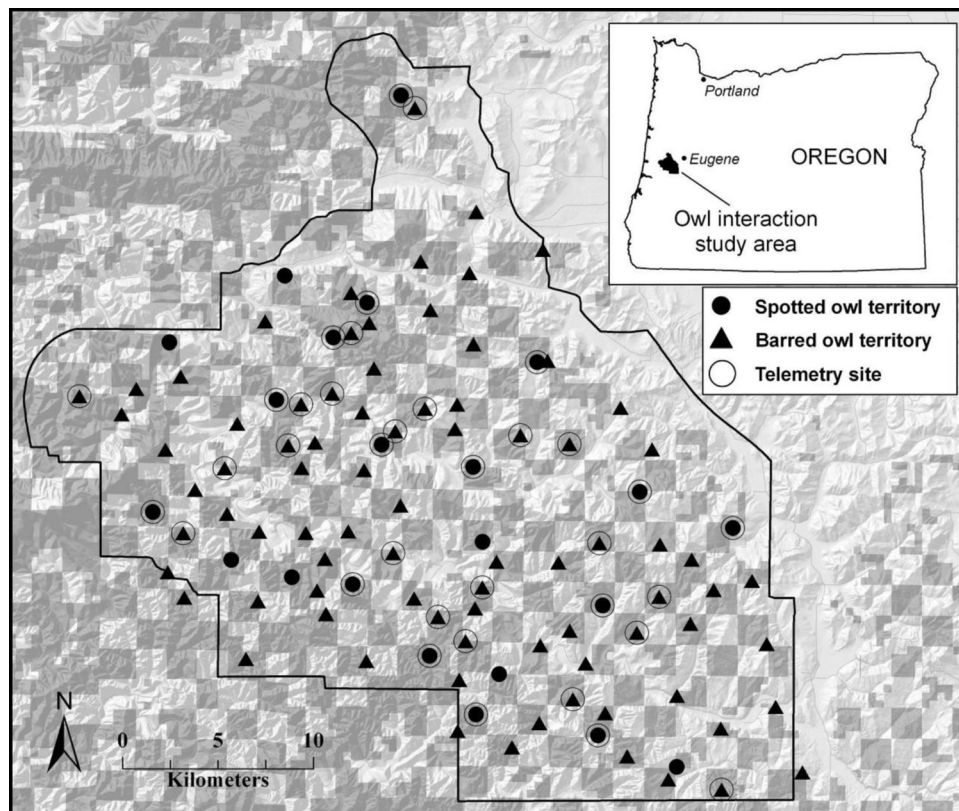


Figure 1. Distribution of territory centers occupied by northern spotted owls and barred owls on the owl interaction study area in western Oregon, USA, 2007–2009. We also show sites where ≥ 1 owl was radio-marked. Dark gray areas indicate federal or state ownership and light gray areas indicate private or county lands.

METHODS

Data Collection

Owl surveys.—We conducted annual surveys of spotted owls and barred owls between 1 March and 1 September 2007–2009. Each year, we used a 2-stage survey protocol to locate both owl species and collect information on site occupancy and reproduction. In the first stage, we used a standardized survey protocol for locating and monitoring spotted owls (Lint et al. 1999) that included ≥ 3 nighttime surveys of areas extending 2.0–2.5 km from historically occupied activity centers (i.e., a nest tree, observations of fledged young, or a pair of resident owls). We conducted annual surveys on as many as 52 territories that were historically occupied by spotted owls, which encompassed 88% of mature and old forests in the study area. In the second stage of our protocol, we used barred owl calls to survey territories found to be occupied by spotted owls. This stage of our survey protocol helped increase the likelihood of detecting barred owls that were spatially associated with territorial spotted owls, and it typically included 1–3 nighttime surveys of an area extending 1.5–2.0 km from a nest or roosting location used by ≥ 1 spotted owl. Further details on the survey protocols we used for each owl species are provided elsewhere (Lint et al. 1999, USFWS 2009, Wiens et al. 2011).

We established a smaller 745-km² study area within the broader telemetry study area in which we systematically surveyed for barred owls in 2009. Repeated surveys of barred owls in 2009 resulted in a high probability of detection (96%) and provided a measure of the occupancy patterns and distribution of territorial pairs of barred owls in the study area (Wiens et al. 2011). We were unable to survey the entire study area for spotted owls, but we estimated that we surveyed $>80\%$ of suitable spotted owl habitat (as defined by Davis et al. 2011) in each year. Moreover, because both owl species were responsive to broadcasts of heterospecific calls, we were confident that we detected most territories occupied by spotted or barred owls during the 3-year study. Once owls were identified as residents and radio-marked, we excluded their territories from conspecific surveys but continued to survey their territories for the presence of the other species.

Radio-marking and tracking.—We attempted to capture and attach radio transmitters to all resident spotted owls located in the study area except for banded owls that were part of adjacent studies of demography (Anthony et al. 2006, Forsman et al. 2011). We captured spotted owls with noose poles as described by Forsman (1983). Once we confirmed the location and residency status of single or paired spotted owls, we attempted to capture and radio-mark all neighboring barred owls identified within a 2.0-km radius. To capture barred owls, we used an amplified megaphone (Wildlife Technologies, Manchester, NH) to broadcast conspecific calls and lure owls into dho-gaza mist nets baited with a mounted specimen of a barred owl or a live mouse (Bierregaard et al. 2008). We fitted all captured owls with a United States Geological Survey (USGS) aluminum leg band. We used a Teflon tubing harness to attach a backpack-style radio transmitter to each owl (Guetterman et al. 1991). Radio transmitters were equipped with a fatality sensor and had a 24-month life expectancy (model RI-2C,

Holohil Systems Ltd, Ontario, Canada). Total mass of radio transmitters (12.5 g with harness) represented 2.2% and 1.9% of mean body mass for male spotted owls and barred owls, respectively. We determined sex of owls based on their vocalizations, nesting behaviors, or measurements (Forsman 1983, Wiens 2012). We recaptured radio-marked owls at the conclusion of the study to remove radio transmitters. We performed all field activities in accordance with Oregon State University's Animal Care and Use Committee (Study No. 3516).

We monitored radio-marked owls using directional 2- or 3-element Yagi antennas (Wildlife Materials, Inc., Carbondale, IL or Telonics, Inc., Mesa, AZ) and a portable receiver (model R-1000, Communication Specialists, Inc., Orange, CA). We estimated nighttime locations of each individual owl ≥ 2 times weekly by taking bearings on the strongest signal received from ≥ 3 different locations spaced >200 m apart within the shortest time possible (≤ 20 min), as described by Carey et al. (1989) and Glenn et al. (2004). We entered signal bearings on site into Program Locate III (Pacer Computing, Tatamagouche, Canada) to estimate a 95% confidence ellipse for the point location (Nams 2006). If a 95% confidence ellipse was >2 ha or if the owl moved before ≥ 3 bearings were taken, we discarded the location and estimated a new location later that night. We used a rotating monitoring schedule to track owls at randomly selected times between sunset and sunrise to ensure that estimated locations were representative of nighttime activities. We also obtained visual observations of all owls at their daytime roosting locations at least once per week to collect pellets and measure roost-site characteristics. We classified locations as either nighttime foraging locations (collected from 0.5 hr after sunset to 0.5 hr before sunrise) or daytime roosting locations, but these classes included a broad range of behaviors beyond foraging and roosting. Each time we obtained locations of owls in a territory, we attempted to locate all radio-marked owls in adjacent territories. In most situations, we relocated spotted and barred owl pairs occupying adjacent territories (4 individuals) within a span of 1.0–1.5 hours. Our goal was to collect ≥ 50 locations per owl each season or 6-month interval.

The extensive road system and high ridges in the study area allowed us to estimate most locations from within 250 m of radio-marked owls, which helped reduce error associated with locations estimated by triangulation (White and Garrott 1990). We estimated the accuracy of the telemetry system by placing radio transmitters at random locations and heights (1–15 m above ground) within owl home ranges and having naïve observers triangulate on them at night. Median linear measurement error between triangulated locations and actual transmitter locations was 78 m (mean = 145 m, SE = 30.7 m, $n = 32$), which was comparable to error estimates in previous telemetry studies of spotted owls (range = 68–164 m; Carey et al. 1992, Zabel et al. 1995, Glenn et al. 2004, Forsman et al. 2005). We used the 95% confidence ellipse estimated for each location in Locate III as a measure of precision of the telemetry system. Median size of the 95% confidence ellipse for triangulated locations was 0.63 ha (mean = 0.74 ha, SD = 0.63 ha), and 99.5% of all nighttime foraging locations for both species had a confidence ellipse ≤ 2 ha.

Quantifying habitat conditions.—Distinctions between the terms habitat, habitat use, and habitat selection are often unclear

(Peek 1986, Block and Brennan 1993, Hall et al. 1997). Similar to Hall et al. (1997), we defined habitat as a distinctive set of resources and conditions present in an area that produce occupancy—including survival and reproduction—by spotted owls or barred owls. We referred to habitat use as the way in which individuals used a collection of physical and biological resources within a defined area and time, and habitat selection as a hierarchical, nonrandom process involving innate and learned decisions made at different geographic scales leading to occupancy or use of a particular location (Hall et al. 1997, Manly et al. 2002). Investigations of resource selection, which require tenuous assumptions about an animal's sensory and decision-making abilities in choosing among available resources, can be approximated by examining variation in resource use (Manly et al. 2002, Kertson and Marzluff 2010). In this study, we measured habitat use by individual spotted owls and barred owls to infer the relative importance of different habitat components to each species and gain an understanding of how resource availability influences perception of resource selection or choice.

We compiled a series of digital maps of primary forest types and physiographic conditions in ArcGIS (version 9.3.1; Environmental Systems Research Institute, Inc., Redlands, CA) to quantify environmental conditions used for foraging and roosting by each owl species. The spatial extent of our maps was based on the cumulative movements of radio-marked owls, where we

identified 5 general forest structural types: old conifer (>120 yr); mature conifer (60–120 yr); young conifer (<60 yr); riparian-hardwood forest, and nonforest (Table 1). Based on previous studies of habitat use by spotted owls (Carey et al. 1992; Glenn et al. 2004; Irwin et al. 2007, 2011) and barred owls (Hamer et al. 2007, Singleton et al. 2010), we identified 9 additional environmental variables to include in our assessment (Table 1). These variables represented forest structural characteristics, physiographic conditions, and interspecific influences that we predicted to be determinants of resource selection.

Satellite maps of forest vegetation in our study area (Ohmann and Gregory 2002) contained useful forest structural information but did not have appropriate spatial resolution to depict landscape features (e.g., stand edges) that we predicted to affect resource selection of owls and their prey. Consequently, we developed a new map of forest types and boundaries from high-resolution (1-m) natural color orthophotographs of the study area (2009 data; USDA National Agricultural Imagery Program [NAIP], Salt Lake City, UT). Specifically, we used object-based classification techniques in ENVI EX image analysis software (version 4.8; ITT Visual Information Solutions 2009) to derive patch-scale maps of the 5 primary forest types described above. This process allowed us to segment the NAIP imagery into clusters of similar neighboring pixels (i.e., objects) and then classify each cluster according to its spatial, spectral, and textural

Table 1. Environmental features used to characterize resource use by sympatric northern spotted owls and barred owls in western Oregon, USA, 2007–2009.

Environmental feature	Abbreviation	Description
Forest cover type ^a		
Old conifer	OLD	Multilayered forests of large Douglas-fir, western hemlock, and western redcedar with dominant overstory trees >120 years old and >90 cm dbh
Mature conifer	MAT	Forests of medium-sized Douglas-fir, western hemlock, and western redcedar with dominant overstory trees 60–120 years old and ≥50–90 cm dbh
Young conifer	YNG	Forests of small Douglas-fir, western hemlock, and western redcedar trees <60 years old and 2.5–50 cm dbh. Mostly included even-aged stands managed for timber production on areas that had been clear-cut and replanted on private and federal lands
Riparian-hardwood	HDW	Riparian forests dominated by red alder, bigleaf maple, and variable amounts of western redcedar and Douglas-fir. Also included patches of lowland forest with >60% cover by hardwood trees and shrubs
Nonforest	NON	Recent clear-cuts dominated by bare soil, grasses, shrubs, or seedling trees <2.5 cm dbh. Also included roads, meadows, agricultural lands, and residential areas
Forest structural conditions ^b		
Density of large conifers	TPHcon50	Density of all live conifers ≥50 cm dbh (trees/ha)
Basal area of hardwoods	BAhdw	Basal area of all live hardwoods ≥2.5 cm dbh (m ² /ha)
Quadratic mean diameter of conifers	QMDcon	Average quadratic mean diameter of dominant and co-dominant conifers (cm)
Canopy cover of hardwoods	CCOVhdw	Canopy cover of all live hardwoods ≥2.5 cm dbh (%)
Abiotic conditions		
Slope	slope	Slope gradient in degrees, derived from a 10-m resolution digital elevation model using ArcGIS spatial analyst (version 9.3.1)
Distance to edge	dedge	Distance (km) to nearest high-contrast edge between mature or old conifer forest and nonforest
Distance to stream	dstream	Distance (km) to nearest permanent stream or river, extracted from the United States Geological Survey National Hydrography Dataset, Oregon (USGS 2010)
Distance to nest	dnest	Distance (km) to nest tree or mean center of daytime roost locations used during the breeding season. This year-specific variable accounted for nonuniform use of space within the home range
Interspecific conditions		
Proximity to heterospecific core-use area	dHET	Distance to nearest heterospecific breeding season core-use area (km). We delineated core-use areas as the area of concentrated use by radio-marked owls or the area within a 620-m (barred owls) or 800-m (spotted owls) radius of the activity center used by unmarked owl pairs
Heterospecific core-use area	HETcore	Discrete variable for locations that were inside (1) or outside (0) the perimeter of a heterospecific neighbor's core-use area

^a We derived forest cover types from object-based classification of 1-m resolution aerial imagery taken in 2009 (Wiens 2012).

^b We derived forest structural conditions from regional maps of vegetation composition and structure (Ohmann and Gregory 2002; www.fsl.orst.edu/lemma), calculated as the mean of 30-m × 30-m pixel values contained within delineated forest patches.

attributes (Hay et al. 2005, Cleve et al. 2008, Blaschke 2010). Thus, contiguous stands of trees with similar size and age (i.e., patches) were represented as polygons with boundaries that matched forest edges shown by the orthorectified imagery. Our minimum mapping unit was 0.5 ha, and mean patch size of the final 2009 vegetation map was 14.0 ha (SD = 41.1 ha, $n = 7,091$ patches). Overall accuracy of the vegetation map was 82% based on ground sampling of vegetation conditions at 141 random test plots (Wiens 2012). The greatest source of mapping error was in distinguishing between young and mature forest types, with mature forest being misclassified as young in 9 (38%) of 24 test plots (Appendix A). Based on these results, we concluded that the mean accuracy of triangulated telemetry locations (0.63 ha) was sufficient to assign locations to polygons of forest cover with negligible error.

The vegetation map that we developed provided a broad-scale representation of the spatial distribution of different forest types but lacked many of the fine-scale structures associated with forest patches that could affect habitat use of owls and their prey. Consequently, we quantified the structural conditions of each patch using data obtained from a regional map of forest vegetation developed using a gradient-nearest-neighbor (GNN) method (Ohmann and Gregory 2002). Specifically, we estimated density (trees/ha) of large (>50 cm dbh) conifers, average quadratic mean diameter of conifers, basal area of hardwoods, and canopy cover of hardwoods as the mean of 30-m $\times$ 30-m GNN pixel values contained within each patch of our forest vegetation map. Local-scale accuracies reported for the 4 GNN variables we used showed that predicted values corresponded well with observed plot measurements ($r = 0.53$ – 0.71 ; Ohmann and Gregory 2002). The GNN map we used was based on satellite imagery from 2006, whereas our forest cover map was based on NAIP imagery from 2009. To account for this mismatch, we obtained time-specific data on timber harvests and used this information to add or subtract vegetation in the 2009 base map.

Owl diets.—We estimated composition, diversity, and overlap of spotted owl and barred owl diets from regurgitated pellets. Pellets were collected from both species by 1) tracking radio-marked owls to their roost sites and searching the ground below their roosts; 2) regularly searching areas of concentrated use by radio-marked owls; 3) searching areas immediately surrounding occupied nests; and 4) climbing nest trees to collect pellets ejected by young inside the nest cavity. To avoid double-counting larger prey that appeared in >1 pellet, we combined remains from multiple pellets found at the same roost on the same date into a single sample and did the same for nest-tree collections. We bagged, labeled (date, location, observer), and dried all pellet collections for later identification of prey remains. During the nonbreeding season (Sep–Feb), we limited searches for pellets to roosts of radio-marked owls because we could not be certain that pellets collected in other areas belonged to the focal owl species. Both owl species tended to roost high (>25 m) in the tree canopy during winter, which made pellets more difficult to find because they would often get stuck in the tree or break apart before reaching the ground. Therefore, most prey remains identified in pellets of spotted owls (95%) and barred owls (94%) were from the breeding season (Mar–Aug).

Monitoring survival and reproduction.—We recorded the fate (live, dead) of radio-marked owls by monitoring transmitter signals 2–4 times per week. Individuals that made long-distance movements in winter were generally relocated in <1 week during expanded searches from the ground, so we had few time periods in which we did not know an owl's fate. If a transmitter signal indicated a fatality, we recovered the carcass or remains of the owl to determine the cause of death, usually within 24 hours. We submitted intact carcasses to the Veterinary Diagnostic Lab at Oregon State University, Corvallis, Oregon for necropsy and histopathology analysis.

We estimated reproductive parameters for all spotted owls in the study area following the methods described in Lint et al. (1999). This protocol takes advantage of the fact that spotted owls are relatively unafraid of humans and will readily take live mice from observers and carry mice to their nest or fledged young (Forsman et al. 2011). Barred owls, however, did not readily take mice from observers so the standard protocol for determining nesting status and number of young fledged for spotted owls was largely ineffective for barred owls. Consequently, we obtained nesting information on barred owls by tracking radio-marked females to their nest trees or by repeatedly locating pairs of unmarked owls during the breeding season to determine nest locations and count the number of young that left the nest. This protocol ensured that all territories included in estimates of nesting success had been monitored between egg-laying (1 Mar) and juvenile dispersal (31 Aug) of each year.

Data Analysis

Spatial relationships.—We made a preliminary assessment of both interspecific and intraspecific territoriality among spotted and barred owls by calculating first-order nearest-neighbor distances between activity centers of all owl pairs identified during the 2009 breeding season, when survey coverage was most complete. Nearest-neighbor distances are a commonly used measure of territoriality in birds of prey (Newton et al. 1977, Katzner et al. 2003, Carrete et al. 2006). We defined activity centers for resident pairs of spotted or barred owls based on the best available records for a given year, including: 1) a used (eggs laid) nest; 2) the mean center of roosting locations acquired from radio-marked owls during the breeding season; 3) location of fledged young; or 4) the mean center of repeated diurnal or nocturnal survey detections of owls classified as residents (Lint et al. 1999, Forsman et al. 2011).

We defined a home range as the area regularly traversed by an individual owl during its daily activities and calculated home ranges over seasonal (6-month) and annual (12-month) time frames. We based seasonal estimates on 2 phenological periods: the breeding season (1 Mar–31 Aug) when owls nested and fed young, and the nonbreeding season (1 Sep–28 Feb) when owls were not engaged in breeding activities. We used the kernel UD function in R version 2.10.1 (Calenge 2006, R Development Core Team 2010) to calculate 95% fixed-kernel home range areas (Worton 1989) for seasonal and annual time periods. Fixed-kernel home ranges represented the area, or group of areas, encompassing 95% of the probability distribution for each individual owl. We did not calculate home ranges for owls with <28 locations per season because of instability of kernel estimates

with small sample sizes (Seaman et al. 1999). We used Animal Space Use 1.3 (Horne and Garton 2009) to estimate a smoothing parameter for each fixed-kernel home range using likelihood cross-validation (CV_h ; Silverman 1986, Horne and Garton 2006). We used CV_h to estimate the smoothing parameter because simulation studies have shown that this method outperforms alternative methods such as least-squares cross-validation (LSCV) and produces a better fit with less variability among estimates, especially with sample sizes ≤ 50 (Horne and Garton 2006). Moreover, we found that home ranges estimated using LSCV tended to over-fit the data, which produced highly fragmented, discontinuous home ranges that excluded areas (e.g., young forest or openings) occasionally used by owls as they moved among patches of their preferred forest types. We also calculated 100% minimum convex polygon (MCP) home ranges using Home Range Tools for ArcGIS (Rodgers et al. 2007). The MCP method suffers from a variety of shortcomings (White and Garrott 1990, Laver and Kelly 2010) but was the only home-range estimator that has been consistently used in previous studies of both spotted and barred owls. Consequently, we relied on MCP home ranges for comparative purposes but considered the 95% fixed-kernel smoothed with CV_h to be the most biologically realistic approximation of each owl's space-use patterns.

We used a fixed-effects analysis of variance to compare the size of home ranges between sexes and seasons for each species. We used linear mixed-models (PROC MIXED; SAS Institute, Cary, NC) to evaluate the relative importance of different biological and environmental features on annual movements of radio-marked owls (i.e., size of the 95% fixed-kernel home range). We treated individual owls nested within species as a repeated effect and species, year, current year's nesting status, and variables representing habitat composition within the home range as fixed effects. Our analysis was based on a set of a priori models containing combinations of biologically relevant covariates hypothesized to explain species-specific variation in annual home range size. Of particular interest were models used to examine the prediction that individual spotted owls or barred owls may alter their space-use patterns in response to an increasing likelihood of encountering the other species within their home range. To examine this prediction, we included the probability of heterospecific presence within the home range (see below) as a covariate to home-range size and investigated how this effect varied between species and with habitat composition by comparing models with additive versus interactive effects. Alternatively, annual home-range size of spotted or barred owls may be associated with the landscape distribution of preferred forest types used for foraging (Glenn et al. 2004, Forsman et al. 2005, Hamer et al. 2007). To examine how the distribution of different forest types might influence space use, we used Patch Analyst for ArcGIS (v0.9.5; Elkie et al. 1999) to estimate proportions of old conifer and riparian-hardwood forest within each owl's home range. We combined old and mature forest types into a single category of older forest (i.e., conifer forest >60 yr old) to test if the combined cover of these 2 forest types influenced space use. We used the second-order Akaike's Information Criterion (AIC_c) to rank candidate models (Burnham and Anderson 2002). Specifically, we made model

comparisons with ΔAIC_c (i.e., the difference between the lowest AIC_c value and AIC_c from all other models), and we used normalized AIC_c weights to evaluate the strength of evidence for each model considered. We considered models with $\Delta AIC_c < 2.0$ to be competitive. We evaluated the degree to which 95% confidence intervals of regression coefficients (β) overlapped 0 to determine the direction, precision, and strength of evidence for covariate effects.

We estimated areas of concentrated use during the breeding season (core-use areas) for individual owls that exhibited a nonrandom pattern of space-use within their home range. We defined the core-use area as the portion of the fixed-kernel breeding season home range in which use exceeded that expected under a null model of a uniform distribution of space-use (Bingham and Noon 1997, Powell 2000, Vander Wal and Rodgers 2012). We estimated core-use areas using Animal Space Use for ArcGIS (Version 1.0, www.gce-lter.marsci.uga.edu/public/app/resource_detail.asp?id=355, accessed 25 Apr 2010). Core-use areas only provide a fraction of the resources required for reproduction and survival, but these areas typically contain unique structures and resources required for nesting, roosting, and provisioning young (Bingham and Noon 1997, Glenn et al. 2004). Hence, we assumed that core-use areas represented the portion of the home range that was likely to be the most heavily defended from conspecifics. In cases where we monitored both male and female members of a pair, we estimated the pair's breeding home range or core-use area as the union (total area) of female and male estimates (Bingham and Noon 1997, Forsman et al. 2005).

We estimated the extent of spatial segregation and space-use sharing among radio-marked owls during annual, breeding, and nonbreeding time frames using 3 complementary overlap statistics: amount of home range overlap (HR), probability of spatial overlap (PHR), and the utilization distribution overlap index (UDOI; Fieberg and Kochanny 2005). We calculated each measure at 2 levels of use intensity within the fixed-kernel home range (95% and 50% utilization contours). We used these measures as indicators of the extent and magnitude of space-use sharing among individual owls as well as their interaction potential (Fieberg and Kochanny 2005). Following the notation of Kernohan et al. (2001), the proportion of owl i 's home range that was overlapped by owl j 's home range was calculated as $HR_{ij} = A_{ij}/A_i$, where A_i is the area of owl i 's home range and A_{ij} is the area of overlap between the home ranges of the 2 owls. We used estimates of HR to delineate the region of spatial overlap between 2 owls, but this measure did not account for the gradient in use intensity within home ranges (i.e., the utilization distribution [UD]). Thus, to provide a more accurate measure of spatial overlap that considered each owl's UD, we calculated the probability of owl j being present in owl i 's home range as:

$$PHR_{ij} = \iint_{A_i} \widehat{UD}_j(x, y) dx dy$$

where $\widehat{UD}_j(x, y)$ was the estimated value of the UD of owl j at location x, y . Estimates of PHR provided an easily interpretable, directional measure of spatial overlap that accounted for differences between individuals in the probability of use within the region of home-range overlap. Estimates of HR and PHR

were directional in that they resulted in 2 values for each dyad combination (i.e., overlap of owl j on owl i 's home range and overlap of owl i on owl j 's home range).

We calculated the UDOI described by Fieberg and Kochanny (2005) to quantify the level of joint space-use sharing among individual radio-marked owls and provide a symmetrical measure of space-use sharing:

$$\text{UDOI} = A_{ij} \iint_{x,y} \widehat{\text{UD}}_i(x,y) \times \widehat{\text{UD}}_j(x,y)$$

The UDOI is a function of the product of the UD of 2 owls integrated over the spatial domain of the home-range estimates and measures the amount of spatial overlap relative to 2 individuals using the same space uniformly. Measures of UDOI range from 0 (no overlap) to 1 (complete overlap) except in cases where the 2 UD are nonuniformly distributed and have an unusually high degree of overlap, in which case UDOI is >1 . The UDOI is nondirectional in that it provides a single measure of space sharing within the overlap region. High intensity use of the same area by 2 owls will result in high UDOI values. Thus, we considered the UDOI to be a good indicator of interaction potential between owls. All measures of spatial overlap were based on the assumption that the fixed-kernel UD smoothed with likelihood cross-validation was an accurate and precise estimate of each owl's space use. We used the *adehabitat* package in R (Calenge 2006, R Development Core Team 2010) to calculate values of HR, PHR, and UDOI for all intraspecific (paired owls, conspecific neighbors) and interspecific (heterospecific neighbors) pairwise combinations. We calculated a mean overlap value for directional measures of overlap by using all possible dyad combinations.

Habitat use.—We evaluated habitat use by spotted owls and barred owls at 2 spatial scales corresponding to Johnson's (1980) second- and third-orders of selection and Block and Brennan's (1993) recommended spatial scales for avian habitat analyses. These 2 spatial scales reflected an owl's use of forest patches within the study area (second-order selection) and use of patches within the home range (third-order selection), respectively. We evaluated habitat use at both scales, but recognized that the territory or home range was the scale at which interspecific interactions were most likely to influence 1 or both species. Accordingly, we described general habitat characteristics used for foraging and roosting within the study area (second-order selection) and developed more detailed, species-specific resource selection functions (RSFs) to explore how environmental conditions and the presence of competitors may influence each owl's selection of foraging locations within the home range (third-order selection).

At the scale of the study area (second-order selection), we compared patterns of habitat use by each species using univariate selection ratios ($\hat{w}_i$) and Bonferroni 95% confidence intervals calculated with the *widesII* function in R (Calenge 2006, R Development Core Team 2010). Specifically, we compared foraging or roosting locations of each owl (used) to 11,974 random points drawn from the analysis region (available) with a type II study design (sampling protocol A; Thomas and Taylor 1990, Manly et al. 2002). Thus, use of resources was

uniquely measured for each owl but occurrence of resources (i.e., availability) was measured at the population (study-area) level. Following Manly et al. (2002:65–67), we calculated selection ratios for each owl as: $\hat{w}_i = O_i/\pi_i$, where $\hat{w}_i$ is the selection ratio for a given resource category i , expressed as the ratio of the sample proportion of used locations, O_i , to the sample proportion of available locations, π_i . A mean selection ratio with a confidence interval >1 indicated positive selection for a particular resource category, and a mean and confidence interval <1 indicated avoidance. We calculated selection ratios for each activity period (daytime, nighttime) using covariates for forest type, distance to edge, distance to stream, and interspecific proximity (Table 1). We used the Jenks natural-breaks method (Jenks 1967) in ArcGIS to divide continuous variables into classes for categorical univariate analyses and plotted overlap of 95% Bonferroni confidence intervals to identify differences in $\hat{w}_i$ between species and activity periods. We also used selection ratios with Pianka's (1973) measure of niche overlap to approximate the level of similarity among neighboring spotted owls and barred owls in their proportional use of different forest types for foraging. This symmetric index ranges from 0 (no overlap) to 1 (complete overlap) and was calculated for each radio-marked spotted owl and the nearest concurrently radio-marked barred owl with sufficient data (>30 nighttime locations). High overlap values indicated that proportional use of different forest types by individual spotted and barred owls in adjacent territories was similar. We calculated the average pairwise overlap among neighboring spotted and barred owls to obtain a mean estimate for our study population.

At the home-range scale (third-order selection), we developed an RSF of nighttime habitat use for each species using the discrete-choice model (Cooper and Millspaugh 1999, Manly et al. 2002, McDonald et al. 2006). Similar to logistic regression analysis, discrete-choice methods assume that animals make a series of selections from finite sets of available resources. Discrete-choice differs from other types of resource selection analyses in that 1) the composition of choice sets may vary among choices, and 2) the analysis estimates the relative probability of a single resource unit being selected during 1 choice rather than across multiple choices (McDonald et al. 2006). These properties of the model allowed us to account for changes in habitat conditions (e.g., timber harvests, presence of competitors) that occurred within many of the owl's home ranges during the study. The discrete-choice RSF has been applied in several previous studies of resource use by spotted owls (McDonald et al. 2006; Irwin et al. 2007, 2011), which facilitated comparisons. Similar to these studies, we developed a choice set for each owl based on the occurrence and use of resources measured within the 95% fixed-kernel home range. This design was analogous to a type III study design in which we compared nighttime foraging locations to 4 times as many random points within the home range (Manly et al. 2002). We chose a multiplier of 4 because it provided a reasonable estimate of the occurrence of different habitat components within home ranges without overly contaminating used with random locations (Johnson et al. 2006). We developed a new choice set for each owl that was monitored >1 year to accommodate annual changes in space use, resource occurrence, and location of potential competitors.

We estimated log-likelihood values and parameter coefficients using a stratified Cox proportional hazards function in SAS 9.3 (PROC PHREG), which uses the same multinomial logit likelihood function as the with-replacement discrete choice model described by Manly et al. (2002). We calculated selection ratios from model coefficients (selection ratio = $\exp[\text{coefficient}]$) to measure the multiplicative change in the relative probability of use when a covariate changed by 1 unit, assuming all other variables remain constant (McDonald et al. 2006, Irwin et al. 2011). We originally modeled sexes separately because of a potential lack of independence among paired males and females in patterns of habitat use. Initial results from sex-specific analyses differed little from an analysis in which sexes were combined, however, so we report results from the latter method for clarity.

We used an information-theoretic approach (Burnham and Anderson 2002) to evaluate candidate models representing alternative hypotheses about the influence of environmental conditions and interspecific interactions on each species' patterns of resource use (Appendix C). We used AIC values to rank models, and we evaluated the degree to which 95% confidence intervals for regression coefficients (β) overlapped 0 to determine the direction, precision, and strength of covariate effects. We used a Pearson correlation matrix to screen habitat covariates for evidence of collinearity and discarded models with highly correlated ($r > |0.5|$) variables. Continuous variables representing forest structural characteristics (e.g., basal area of hardwoods) were correlated with the classified forest cover map (e.g., hardwoods), so we did not include the forest type variable and covariates representing forest structural conditions in the same model. We then fit a base RSF for each species using forest type, forest structure, and abiotic covariates only (Table 1). Once we attained a final base model for each species, we used ΔAIC values to determine whether the addition of covariates related to heterospecific presence improved model fit, and hence whether heterospecific neighbors affected resource use. Covariates representing heterospecific presence were 1) distance to the nearest heterospecific core-use area; and 2) a binary variable for locations inside or outside of a heterospecific core-use area (Table 1). Based on estimates from radio-marked owls in our study, we used 620-m and 800-m radius circles centered on year-specific activity centers to represent areas of concentrated use by unmarked pairs of barred owls and spotted owls, respectively. Under a hypothesis of interspecific territoriality (Dhondt 2012), we predicted that 1) owls would use sites more distant from heterospecific core-use areas than expected based on occurrence; and 2) owls would use areas more distant from their preferred forest types when heterospecifics were present.

We also wanted to identify differences between the species in use of specific resource components and to quantify the uncertainty associated with those differences. We pooled the nighttime telemetry data from both species and fit 4 additional discrete-choice models that considered an interactive effect of species with environmental covariates included in the best models developed for each species separately. Better support of models including interactive effects relative to models without interaction terms provided evidence for differential resource use, and regression coefficients with 95% confidence intervals provided evidence for which environmental conditions differed between

species. As in previous analyses, we used AIC to rank competing models.

Dietary analysis.—We identified prey remains from owl pellets using dichotomous keys and a reference collection of bird and mammal skeletons at the United States Forest Service Pacific Northwest Research Station, Corvallis, Oregon, USA. Remains that could not be identified to species were identified to the lowest taxon possible. We quantified dietary composition using standard measures of relative frequency and biomass (Ganey and Block 2005, Marti et al. 2007). We estimated the frequency of vertebrate prey items in diets by counting skulls, mandibles, or bones of the appendicular skeleton, whichever gave the highest count (Forsman et al. 2001, 2004; Hamer et al. 2001). For invertebrates, we estimated numbers based on fragments of the exoskeleton or shells following Graham (2012). We used owl territories as the primary sampling unit in dietary analyses to avoid biases associated with an unequal number of prey remains collected for different owl pairs and to allow estimation of the amount of dietary variation among territories (Seamans and Gutiérrez 1999, Forsman et al. 2004). Thus, we characterized dietary composition for each species by computing the percent of prey numbers and percent of prey biomass in samples from each territory and then averaging among territories. Mean estimates of dietary composition were based on territories with ≥ 20 prey items.

We subdivided diets into 30 prey types for comparisons of dietary composition between spotted and barred owls. These categories were based on those described for spotted owls by Forsman et al. (2004) in addition to prey types that contributed $>2\%$ of total prey numbers to diets of barred owls. We estimated the percent composition of prey identified in pellets from each territory by dividing the estimated number of individuals of each prey species by the total number of prey in the sample and multiplying by 100. To estimate the percent of total biomass for each prey species in the diet of each territory, we divided the estimated total biomass of each species by the total biomass in the sample and multiplied by 100.

We used 2 different methods to estimate the total biomass of each prey species in the diet, depending on the type of prey. For smaller prey (e.g., insects, shrews, mice, voles), we multiplied the estimated number of individuals of each species by the estimated mean mass of each species. We obtained estimates of mean mass from a variety of sources, including Dunning (1993) for birds and Verts and Carraway (1998) for most mammals. For larger species, such as northern flying squirrels (*Glaucomys sabrinus*), snowshoe hare (*Lepus americanus*), brush rabbits (*Sylvilagus bachmani*), woodrats (*Neotoma* spp.), mountain beaver (*Aplodontia rufa*), and ruffed grouse (*Bonasa umbellus*), we estimated mass of each individual based on comparisons of bones from specimens of known mass in the reference collection. Specifically, we measured mass and bone size of juveniles and adult specimens of these species and made the simplifying assumption that mass was linearly correlated with bone size (Forsman et al. 2004). We then summed the individual estimates to get the total biomass for each species. We used this method to prevent overestimating biomass of large prey represented by both adults and small juveniles in our sample. We estimated mean mass of signal crayfish (*Pacifastacus leniusculus*) from samples of locally collected specimens

(Graham 2012). To further evaluate potential differences in the timing and location of foraging by spotted and barred owls, we grouped prey species by their primary period of activity (nocturnal, diurnal, or both) and primary zone of activity (aerial, arboreal, semi-arboreal, terrestrial, or aquatic). Behavioral attributes of prey in our study area were based on information in Verts and Carraway (1998), Hamer et al. (2001), and Forsman et al. (2004). We used a contingency test of independence to evaluate differences between species in the frequency of prey captured that were in different behavioral categories.

We used 3 standard trophic estimators for comparisons of prey numbers in diets of each owl species: food niche breadth, mean prey mass, and food niche overlap (Marti et al. 2007). We estimated food-niche breadth (FNB), an index of diversity in owl diets, using the reciprocal of Simpson's index (Simpson 1949, Levins 1968). Values of FNB ranged from 1 to n , where n was the total number of prey types (30 in our case). For comparisons between owl species, we standardized FNB to a proportion following Colwell and Futuyma (1971): $FNB_{st} = (FNB - 1) / (n - 1)$. We estimated values of FNB and FNB_{st} for each owl territory and then averaged among territories for interspecific comparisons. Measures of FNB are dependent on sample size and how the diet data are categorized, so we used an individual-based rarefaction analysis (Heck et al. 1975, Gotelli and Colwell 2001) to statistically compare differences in prey species richness between the diets of spotted and barred owls. We estimated expected species richness as the mean number of prey species present over repeated randomized subsamples of each species' observed diet. We used the species diversity module in program EcoSim 7.71 to estimate mean expected prey species richness and 95% confidence intervals in increments of 20 prey items (Gotelli and Entsminger 2004). We estimated mean mass of prey captured by each owl pair by dividing the total biomass in the sample by the total number of prey in the sample. We estimated mean prey mass with and without insect prey included because of a high frequency of insects in diets of barred owls. For comparisons between species according to the size of prey captured, we divided prey into 7 classes according to mean mass and calculated the frequency of occurrence in each class for each owl pair.

We used Pianka's (1973) index of niche overlap as a measure of dietary overlap between each pair of spotted owls and the nearest neighboring pair of barred owls with sufficient data (≥ 20 prey items). We used program EcoSim to generate null expectations of food-niche overlap (Gotelli and Entsminger 2004), which provided a baseline measure in evaluating the observed level of interspecific dietary overlap. Specifically, we compared observed values of dietary overlap with the expected frequency distribution of overlap values generated from 2,000 Monte Carlo randomizations of the observed diet data. Null models provided an appropriate null hypothesis against which the observed values of food-niche overlap could be compared (Gotelli and Graves 1996). We constructed null models using Lawlor's (1980) randomization algorithm 3, which retained the realized niche breadth of each owl species while randomizing proportional use of different prey categories. In addition, we compared proportions of prey consumed by owls during breeding and nonbreeding seasons to evaluate the potential for seasonal

changes in dietary composition and overlap. Seasonal analyses were based on the combined sample for all owl pairs because samples were too small to estimate diets of owl pairs in the nonbreeding season.

Trophic and ecological overlap.—After calculating overlap coefficients between the 2 species along the resource axes of space (home ranges and core-use areas), habitat (use of primary forest types), and food (diet composition) separately, we then calculated a single measure of ecological overlap as the arithmetic mean of spatial, habitat, and dietary overlap coefficients (May 1975, Geange et al. 2011, Whitney et al. 2011). Values of ecological overlap were 0 when distributions of space-use, habitat use, or diets were completely disjoint and 1 when they completely overlapped. In addition, we calculated trophic overlap by multiplying habitat and dietary overlap coefficients (MacArthur and Levins 1967, Pianka 1974, Whitney et al. 2011). We calculated overlap coefficients for each radio-marked spotted owl and the nearest barred owl that was concurrently radio-marked. If >1 barred owl home range overlapped with the focal spotted owl, we selected the barred owl with the greatest cumulative home-range overlap. We were unable to estimate diets of individual owls directly because pellets of males and females were often mixed under roosts, so individuals assumed territory-specific values of dietary overlap in calculations of trophic and ecological overlap. Taken together, trophic and ecological overlap values provided an index of the variation among individuals in their potential exposure to exploitative competition with neighboring heterospecifics.

Estimation of survival probabilities and reproduction.—We used known-fate models in Program MARK (White and Burnham 1999) to estimate survival probabilities of radio-marked owls and to assess the influence of time, sex, habitat conditions, and interspecific interactions on species-specific survival. Known-fate parameter estimation in program MARK uses a modification of the Kaplan–Meier product limit estimator (Kaplan and Meier 1958) that accommodates staggered entry of individuals as they are added or censored from the risk set (Pollock et al. 1989). We conducted the survival analysis in 2 steps. First, we evaluated support for a set of 10 a priori models that considered species- and sex-specific variation in seasonal (6-month), annual (12-month), and cumulative (22-month) survival probabilities. Second, we introduced a small number of biologically relevant covariates to the most parsimonious model from step 1. This stage of the analysis was based on a small set of models developed to examine alternative hypotheses regarding the influence of forest conditions, interspecific interactions, and a combination of these effects on survival of each species (Appendix D). We modeled species jointly to examine species-specific differences in covariate relationships by allowing slope coefficients to vary between species via an interaction term. We selected the best models using AIC_c (Burnham and Anderson 2002).

We selected 5 spatially explicit covariates to include in known-fate models of survival for spotted and barred owls. Several studies have identified associations between survival of spotted owls and the amount of old forest in their territories (Franklin et al. 2000, Olson et al. 2004, Dugger et al. 2005). To examine how this relationship might vary between spotted and barred

owls, we tabulated the proportion of old (>120 yr) conifer forest in seasonal 95% fixed kernel home ranges and core-use areas of radio-marked owls. Similar to anecdotal evidence from previous studies in western Oregon (Forsman et al. 1984, Paton et al. 1991, Carey et al. 1992), predation by great horned owls (*Bubo virginianus*) appeared to be a primary source of mortality for spotted owls in our study area. Great horned owls often include nonforested openings in their home ranges (Grossman et al. 2008, Ganey et al. 1997) and may generally prefer highly fragmented landscapes for foraging (Johnson 1993). Consequently, we hypothesized that spotted owls that spent more of their time near open areas and habitat edges may have experienced a greater risk of predation than owls that avoided these areas. To evaluate this hypothesis, we calculated the mean distance from used telemetry points for each owl to the closest edge between forested and nonforested areas, and included those values as individual covariates in Program MARK. To investigate the potential influence of spatial interactions with heterospecifics on survival, we included 2 measures of spatial overlap: 1) the mean proportion of each owl's home range that was shared with radio-marked heterospecifics in adjacent territories (HR); and 2) the mean probability of heterospecific presence in the home range (PHR). The spatial variables we used assumed that telemetry locations represented a random sample of use within the home range and that the mean adequately represented exposure to these conditions.

We estimated reproductive output for each species as the number of young fledged per territorial female per year following Franklin et al. (1996), Lint et al. (1999), and Glenn et al. (2011b). Estimates ranged from 0 to 2 for spotted owls and 0 to 4 for barred owls, and included all paired owls that we monitored during 1 March–31 August. We used linear mixed-models (Littell et al. 2006) to examine evidence for a negative association between annual estimates of number of young fledged for spotted owls and proximity to the nearest known barred owl nest or activity center (PROC MIXED, SAS Institute). We treated site (owl territory) and year (a categorical variable) as random effects and the nearest-neighbor distance (km) between breeding activity centers of spotted and barred owls in adjacent territories as a fixed effect. As described above, we surveyed barred owls within all territories occupied by spotted owls in each year of the

study. We therefore considered interspecific nearest-neighbor distances to be an accurate measure of territorial relationships among both radio-marked and unmarked owl pairs. Sample sizes were small ($n = 13$ – 15 spotted owl territories per yr), so we chose not to attempt to model reproduction further and considered this analysis to be exploratory rather than confirmatory. Age can have an effect on demography of spotted owls (Anthony et al. 2006, Forsman et al. 2011). We were unable to age barred owls in our study, but all radio-marked spotted owls were mature adults (≥ 3 yr).

RESULTS

Owl Surveys and Radio Tracking

We identified 18 territories occupied by ≥ 1 spotted owl and 82 territories occupied by ≥ 1 barred owl during 2007–2009 (Table 2). The total number of territories occupied by spotted owls remained relatively stable during the study, ranging from 16 in 2007 to 18 in 2009. In contrast, the total number of detected territories with barred owls increased from 35 in 2007 to 82 in 2009, largely as a result of annual expansions in survey effort for barred owls. By 2009, we had identified a high density of regularly spaced nesting territories occupied by barred owls (Fig. 1). We radio-marked 29 spotted owls (14 F, 15 M) at 15 territories and 28 barred owls (13 F, 15 M) at 21 territories. The sample of spotted owls included 13 territories where both pair members were radio-marked, 2 territories where a single resident male was marked, and 1 territory where we marked a female that paired with a radio-marked male captured in an adjacent territory in the previous year. The sample of barred owls included 6 territories where both pair members were radio-marked and 16 territories where only 1 member of a resident pair was captured. Of the 57 owls that we radio-marked, 47 (24 spotted owls, 23 barred owls) were radio-marked in 2007 and 10 (5 spotted owls, 5 barred owls) were radio-marked in 2008 in areas where spotted owls had not been previously detected.

We attempted to obtain 24 months of data on owls radio-marked in 2007 but were limited by mortality or premature radio-failure (Fig. 2). Cumulative tracking periods averaged 565 days for spotted owls (SD = 193, range = 73–734 days) and 562 for barred owls (SD = 162, range = 109–777 days). We obtained an

Table 2. Results of annual (1 Mar–28 Feb) surveys conducted for northern spotted owls and barred owls in western Oregon, USA, 2007–2009. We also show the number of territories and individual owls under radio-telemetry study.

Year and species	Survey results				Radio-telemetry monitoring	
	Territories surveyed ^a	Territories with pairs (%) ^b	Additional territories ^c	Territories with ≥ 1 owl	Territories monitored	No. owls with transmitters
2007						
Spotted owl	42	14 (33)	0	16	13	24
Barred owl	42	27 (64)	6	35	19	23
2008						
Spotted owl	49	12 (25)	2	17	14	23
Barred owl	49	31 (63)	9	40	19	24
2009						
Spotted owl	52	15 (29)	1	18	12	18
Barred owl	52	48 (92)	32	82	19	23

^a Historical territories occupied by a pair of spotted owls at least once during 1969–2006.

^b Number and percentage of historical territories surveyed that were occupied by owl pairs.

^c Additional territories were those identified in areas >2.5 km from the center of historical territory locations.

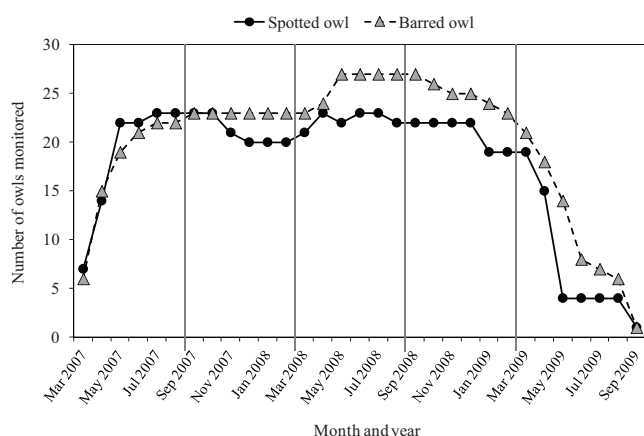


Figure 2. Tracking period for 28 northern spotted owls and 29 barred owls radio-marked in western Oregon, USA, during March 2007–September 2009. Vertical lines indicate 6-month intervals used to distinguish between breeding and nonbreeding seasons.

average of 133 locations per spotted owl (SD = 49, range = 29–201) and 145 locations per barred owl (SD = 42, range = 32–199). The total number of telemetry locations for both species combined was 7,564 (5,809 nighttime foraging locations, 1,755 daytime roost locations). We did not use home range or habitat use data from 3 spotted owls and 1 barred owl that died within the first 110 days of being radio-marked, but these individuals were included in estimates of survival. We also excluded a single male spotted owl from the analysis of habitat use because he spent several months outside of the study area.

Spatial Relationships

Based on the distribution of activity centers for owl pairs in 2009, barred owls established their nesting areas closer to activity centers occupied by spotted owls (mean nearest-neighbor distance [NND] = 1.63 km, range = 0.53–2.98 km, $n = 18$) than to those occupied by other pairs of barred owls (NND = 2.20 km, range = 0.96–4.48 km, $n = 79$; $t_{95} = -3.26$, $P = 0.002$). Compared to barred owls, territories occupied by pairs of spotted owls were sparsely distributed in the study area (NND = 4.53 km, range = 3.21–6.52 km). The minimum distance between 2 concurrently used nest trees of spotted

and barred owl pairs was 0.84 km, which was considerably shorter than the minimum distance between 2 nests used by different pairs of barred owls (1.94 km) or spotted owls (2.27 km).

Space use and seasonal movements.—Home ranges of individual spotted owls during annual, breeding, and nonbreeding periods were 2–4 times larger than those of barred owls (Table 3). This pattern was consistent among individual owls and in cases where we monitored the combined home ranges of paired males and females (Table 4). Although not significant (all P -values > 0.13), male spotted owls tended to have smaller annual home ranges than females, whereas male barred owls tended to have larger annual home ranges than females. Consequently, the largest difference in space-use patterns between the 2 species was for females, with female spotted owls having annual ranges that averaged 4.2 times larger than those of female barred owls. During the breeding season, proportions of different forest types within home ranges and core-use areas of individual spotted and barred owls were similar except that ranges of barred owls tended to include more hardwood forest than those of spotted owls (Table 5). We found no evidence that the size of annual home ranges was correlated with the number of locations for spotted owls ($r = 0.13$, $P = 0.137$) or barred owls ($r = 0.07$, $P = 0.444$).

The best model explaining variation in size of annual home ranges included the effects of owl species, probability of heterospecific presence in the focal individual's breeding home range (PHR), and an interaction between species and PHR (Table 6). This model accounted for 88% of the AIC_c weight and indicated a positive linear relationship between annual home range size of spotted owls and the probability of barred owl presence (Fig. 3). The 95% confidence intervals for the effects of species ($\beta = 785$, SE = 369.5, 95% CI = 42–1,528) and species $\times$ PHR ($\beta = 2,298$, SE = 796.8, 95% CI = 671–3,925) did not overlap 0, indicating that the interaction between these variables contributed significantly to model fit. The second-best model ($\Delta AIC_c = 5.10$) included the additive effects of species, PHR, and amount of old (>120 yr) conifer forest in the home range. The regression coefficient for amount of old forest in this model indicated a negative relationship with home-range size for both owl species, but the 95% confidence interval marginally included 0 ($\beta = -1,915$, SE = 1,150.2, 95% CI = -4,265 to 433). Models containing the effects of year, nesting status, or proportion of

Table 3. Home-range size (ha) of individual northern spotted owls and barred owls in western Oregon, USA, 2007–2009. We calculated home ranges using the 95% fixed-kernel estimator with likelihood cross-validation.

Time period ^a	n (F, M) ^b	All owls			Females			Males		
		Mean	SE	Range	Mean	SE	Range	Mean	SE	Range
Annual										
Spotted owl	26 (12, 14)	2,813	290	754–8,040	3,165	490	767–8,040	2,507	332	754–6,470
Barred owl	27 (13, 14)	879	110	213–4,887	737	77	213–1,367	1,015	201	496–4,887
Breeding										
Spotted owl	23 (10, 13)	1,620	193	217–4,880	1,508	288	217–4,880	1,712	265	341–4,615
Barred owl	26 (12, 14)	556	41	143–1,416	487	57	143–1,111	614	57	265–1,416
Nonbreeding										
Spotted owl	24 (12, 12)	2,688	273	237–7,458	3,008	450	237–7,458	2,351	292	725–4,808
Barred owl	26 (12, 14)	1,028	139	275–5,999	874	114	275–2,144	1,168	243	450–5,999

^a Annual = 1 Mar–28 Feb; breeding = 1 Mar–31 Aug; nonbreeding = 1 Sep–28 Feb.

^b Number of owls included in estimates (females, males).

Table 4. Mean size (ha) of combined male and female home ranges and core-use areas for territorial pairs of northern spotted owls and barred owls during the breeding season (1 Mar–1 Sep) in western Oregon, USA, 2007–2009.

Species	<i>n</i> ^b	100% MCP ^a			95% fixed kernel ^a			Core-use area ^a			
		Mean	SE	Range	Mean	SE	Range	Mean	SE	Range	Proportion ^c
Spotted owl	13	1,881	291	482–4,103	1,843	295	534–4,106	305	59	74–668	0.19
Barred owl	10	581	74	277–1,155	846	72	556–1,318	188	29	85–347	0.22

^a Estimated as the union (total area) of the minimum convex polygon (MCP), 95% fixed-kernel, or core-use area estimated for male and female members of each pair.

We estimated core-use areas as the overused portion of the breeding home range relative to a uniform distribution of space use (Bingham and Noon 1997).

^b Number of owl pairs included in estimates.

^c Size of the core-use area divided by the size of the 95% fixed-kernel home range.

Table 5. Mean proportion of different forest cover types in the core-use area, 95% fixed-kernel home range, and region of spatial overlap between space-sharing northern spotted owls and barred owls during the breeding season in western Oregon, USA, 2007–2009.

Forest type ^a	Species	Core-use area		Home range		Overlap region	
		Mean	SE	Mean	SE	Mean	SE
Old conifer	Spotted owl	0.396	0.026	0.223	0.015	0.293	0.026
	Barred owl	0.335	0.027	0.230	0.019		
Mature conifer	Spotted owl	0.199	0.026	0.213	0.019	0.161	0.016
	Barred owl	0.215	0.023	0.190	0.015		
Young conifer	Spotted owl	0.259	0.029	0.345	0.021	0.368	0.024
	Barred owl	0.299	0.026	0.362	0.023		
Riparian-hardwood	Spotted owl	0.063	0.011	0.055	0.006	0.101	0.014
	Barred owl	0.115	0.020	0.107	0.013		
Nonforest	Spotted owl	0.083	0.094	0.169	0.015	0.080	0.015
	Barred owl	0.036	0.063	0.121	0.016		

^a Proportional forest composition of the study area was 0.170 (old conifer), 0.223 (mature conifer), 0.340 (young conifer), 0.048 (riparian-hardwood), and 0.208 (nonforest).

Table 6. Ranking of mixed-effects models used to examine variation in the size of annual home ranges of northern spotted owls and barred owls in western Oregon, USA, 2007–2009.

Model ^a	<i>K</i>	$-2 \log L$	ΔAIC_c	AIC_c wt
Spp + PHR + (spp × PHR)	8	1,350.6	0.0	0.88
Spp + OLD + PHR	7	1,355.8	5.1	0.07
Spp + PHR	6	1,358.5	5.5	0.06
PHR	4	1,382.6	18.8	0.00
Spp + yr + (spp × yr)	11	1,382.7	32.0	0.00
Spp	5	1,390.0	34.2	0.00
Spp + OLDER + (spp × OLDER)	8	1,385.5	34.8	0.00
Spp + yr	7	1,387.9	34.9	0.00
Spp + OLD + HDW	7	1,385.8	35.1	0.00
Spp + OLD	6	1,388.4	35.3	0.00
Spp + OLDER	6	1,388.6	35.6	0.00
Spp + HDW	6	1,388.7	35.7	0.00
Spp + OLD + (spp × OLD)	8	1,386.4	35.7	0.00
Spp + sex	7	1,389.1	36.1	0.00
Spp + nest	7	1,389.6	36.6	0.00
Spp + sex + (spp × sex)	11	1,387.5	36.8	0.00
Spp + HDW + (spp × HDW)	8	1,388.2	37.5	0.00
Spp + OLD + HDW + (spp × OLD) + (spp × HDW)	11	1,383.8	38.0	0.00
Spp + nest + (spp × nest)	11	1,389.2	38.6	0.00
Spp + sex + nest + (sex × nest)	13	1,388.5	40.2	0.00
Null model (no fixed effects)	3	1,415.0	57.5	0.00
Yr	5	1,413.1	57.9	0.00
Nest	5	1,413.5	58.2	0.00
Sex	4	1,414.4	59.1	0.00
OLDER	4	1,414.4	59.2	0.00

^a Key to model notation: *K* = number of parameters in model (includes intercept and 2 covariance parameters); $-2 \log L$ = value of the maximized log-likelihood function; ΔAIC_c = difference between the corrected Akaike's Information Criterion (AIC_c) value of each model and the lowest AIC_c model; AIC_c wt = Akaike weight; spp = species; yr = year; OLDER = proportion of the home range with conifer forest >60 years old; OLD = conifer forest >120 years old; HDW = riparian-hardwood forest; nest = current year's nesting status; PHR = probability of locating a radio-marked heterospecific neighbor within the focal individual's home range (Fieberg and Kochanny 2005).

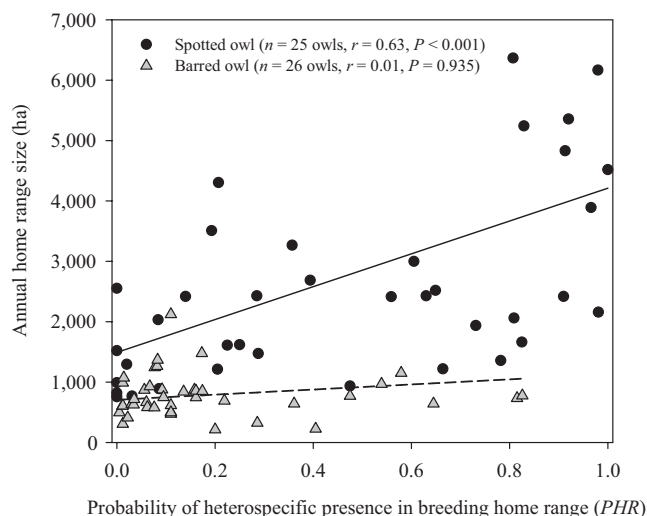


Figure 3. Annual home-range size of individual northern spotted owls was positively associated with the probability of barred owl presence within the breeding-season home range in western Oregon, USA, 2007–2009. This relationship was neutral for barred owls. Prediction lines are from the best-fitting model used to examine variation in annual home range size, which included an interaction term between the effects of species and the probability of heterospecific presence in the breeding-season home range.

hardwood forest in the home range were not supported by the data (AIC_c wt = 0.00; Table 6), and regression coefficients for these effects broadly overlapped 0.

The core-use area of most (94%) individual spotted and barred owls was resolved between the 45–66% fixed-kernel isopleths ($\bar{x}$ = 53%, range = 30–72%), which provided evidence of non-uniform space use within the breeding home range for both species. One female barred owl (paired with young) and 2 male spotted owls (both single residents) exhibited space-use patterns that did not deviate from a uniform distribution, so we did not compute a core-use area for these individuals. Core-use areas of individual owls always contained nest trees or regularly used roosts and averaged 257 ha for spotted owls (SE = 29, range = 37–668 ha, n = 22 owls) and 136 ha for barred owls (SE = 11, range = 40–334 ha, n = 25 owls). Mean size of the core-use area for owl pairs represented 19% and 22% of the total breeding home range used by pairs of spotted owls and barred owls, respectively (Table 4). On average, core-use areas for each species contained similar proportions of older (>60 yr) conifer forest (Table 5), but barred owls tended to have greater proportions of hardwood forest in their core-use areas ($\bar{x}$ = 0.12, SE = 0.02, 95% CI = 0.07–0.16) than spotted owls ($\bar{x}$ = 0.06, SE = 0.01, 95% CI = 0.04–0.09).

Both species used home ranges during the nonbreeding season that were approximately twice as large as those used during the breeding season (Table 3; spotted owls: $F_{1, 21} = 40.90$, $P < 0.001$; barred owls: $F_{1, 24} = 15.80$, $P < 0.001$). Barred owls, however, exhibited a stronger pattern of site fidelity to their nesting areas during the nonbreeding season than spotted owls. Barred owls generally remained within 1–2 km of their nest sites throughout the year, whereas spotted owls were often located 3–6 km from their breeding sites in fall and winter (Fig. 4). Of the 23 spotted owls that were tracked for >1 year, 3 females and 2 males exhibited winter migration behavior in which they

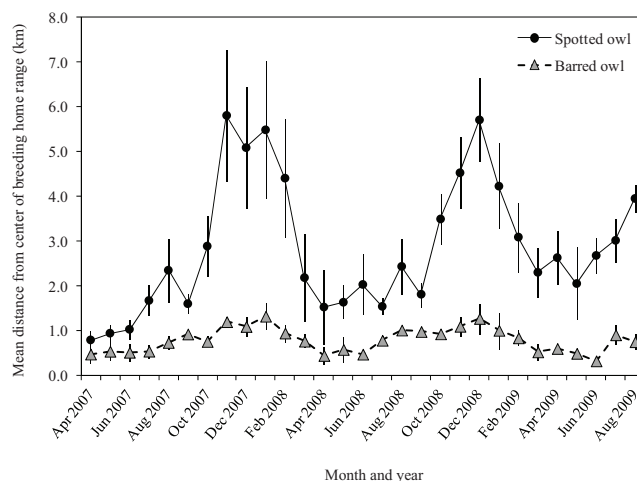


Figure 4. Monthly variation in the mean distance between nighttime foraging locations used by radio-marked northern spotted owls or barred owls and the center of each owl's breeding home range in western Oregon, USA, 2007–2009. We show weighted means and standard errors (vertical bars) estimated from individual spotted and barred owls, subdivided by month. The center of each owl's breeding-home range was the current year's nest location or the mean center of roosting locations used during 1 March–31 August of each year. Estimates do not include incubating females.

established a winter home range that was 7–25 km distant from their breeding range. In contrast, most barred owls (25 of 27 birds) simply expanded their use of space in late fall and winter so that the nonbreeding range largely overlapped the breeding range. The 2 exceptions were cases where individual barred owls (1 M, 1 F) left their territories in early January and moved up to 20–38 km away before returning to the same nesting areas in late February. Such movements were uncommon and only occurred in 1 of the 2 winters in which we tracked these individuals.

Spatial interactions among radio-marked owls.—We observed little intraspecific overlap among home ranges of conspecific owls in adjacent territories, especially during the breeding season when owls were expected to be most strongly territorial (Table 7). For barred owls on adjacent territories, we found no cases of intraspecific overlap among 50% fixed kernel home ranges, and overlap among 95% fixed kernel home ranges was low (HR: $\bar{x}$ = 0.10, range = 0.02–0.23; PHR: $\bar{x}$ = 0.08, range = 0.01–0.29; UDOI: $\bar{x}$ = 0.01, range = 0.00–0.02). Intraspecific overlap among breeding ranges of individual spotted owls on adjacent territories was also low (HR: $\bar{x}$ = 0.13, range = 0.01–0.44; PHR: $\bar{x}$ = 0.11, range = 0.04–0.73; mean UDOI: $\bar{x}$ = 0.02, range = 0.00–0.17, n = 39). Estimates of spatial overlap between home ranges of paired female and male barred owls were consistently high and varied little among breeding and nonbreeding periods (Table 7, Fig. 5). In contrast to barred owls, space-use sharing of paired female and male spotted owls declined during late fall and winter (Fig. 5).

Based on the distribution of territories occupied by marked versus unmarked barred owls (e.g., Fig. 1), the actual number of barred owls that were spatially associated with radio-marked spotted owls was considerably greater than that estimated from radio-marked owls alone. Hence, measures of interspecific overlap reported here reflect average spatial overlap among

Table 7. Seasonal measures of intra- and interspecific home-range overlap among sympatric northern spotted owls (SPOW) and barred owls (BAOW) in western Oregon, USA, 2007–2009. We show the mean proportion of owl i 's home range that is overlapped by the home range of owl j (HR), and the probability of owl j being present in the home range of owl i (PHR).

			Overlap of 95% fixed kernel home ranges ^a				Overlap of 50% fixed kernel home ranges ^a			
			HR		PHR		HR		PHR	
Overlap type	Time period ^b	<i>n</i> ^c	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Intraspecific										
SPOW (paired F and M)	Breeding	26	0.55	0.05	0.71	0.05	0.63	0.06	0.41	0.04
	Nonbreeding	30	0.47	0.05	0.53	0.05	0.30	0.06	0.23	0.04
BAOW (paired F and M)	Breeding	18	0.68	0.05	0.81	0.03	0.58	0.07	0.42	0.05
	Nonbreeding	14	0.68	0.06	0.80	0.04	0.42	0.08	0.36	0.05
SPOW:SPOW	Breeding	39	0.13	0.02	0.11	0.02	0.01	0.01	0.01	0.01
	Nonbreeding	74	0.14	0.02	0.15	0.02	0.05	0.02	0.04	0.01
BAOW:BAOW	Breeding	20	0.10	0.02	0.08	0.02	0.00	0.00	0.00	0.00
	Nonbreeding	48	0.15	0.02	0.11	0.02	0.00	0.00	0.00	0.00
Interspecific										
BAOW:SPOW	Breeding	71	0.38	0.04	0.15	0.03	0.11	0.03	0.03	0.01
	Nonbreeding	115	0.33	0.03	0.11	0.01	0.07	0.02	0.02	0.01
SPOW:BAOW	Breeding	66	0.14	0.02	0.39	0.04	0.04	0.01	0.09	0.02
	Nonbreeding	110	0.11	0.01	0.34	0.03	0.03	0.01	0.06	0.01

^a We calculated mean estimates for intraspecific overlap types using all possible dyad combinations.

^b Breeding = 1 Mar–31 Aug; nonbreeding = 1 Sep–28 Feb.

^c Number of observed overlap combinations used to calculate means.

individuals in adjacent territories rather than cumulative interspecific overlap. Each individual spotted owl shared a portion of its annual home range with 0–8 barred owls in adjacent territories ($\bar{x} = 2.4$ barred owls per spotted owl). The proportion of a spotted owl's annual home range that was shared with a neighboring barred owl (HR) ranged from 0.01 to 0.56 ($\bar{x} = 0.10$, $SE = 0.01$), and the proportion of a barred owl's annual home range that was shared with a spotted owl ranged from 0.01 to 1.00

($\bar{x} = 0.35$, $SE = 0.03$). In several cases, the smaller home ranges of barred owls were completely subsumed within the larger ranges of spotted owls. Measures of interspecific overlap of 50% UD's were low despite a moderate to high level of overlap among 95% UD's. Upon examination of forest composition within areas of interspecific home-range overlap during the breeding season, we found that average proportions of old conifer ($\bar{x} = 0.29$, $SE = 0.03$) and hardwood forest ($\bar{x} = 0.10$, $SE = 0.01$) were

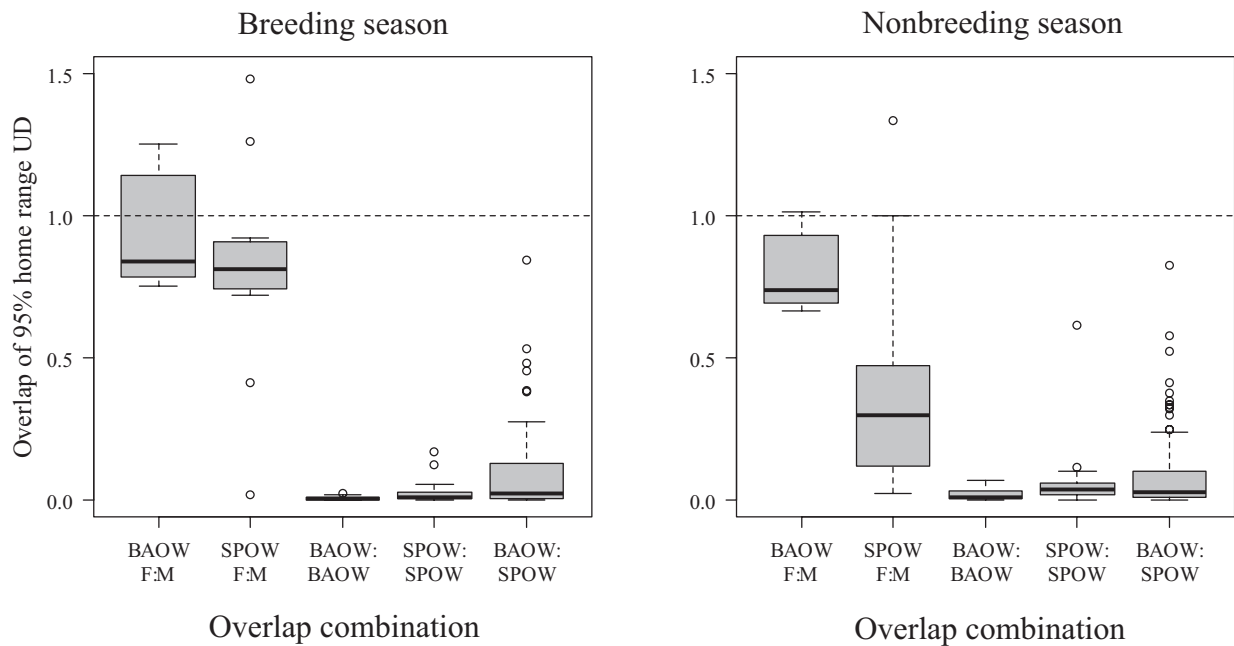


Figure 5. Intra- and interspecific overlap among the 95% fixed-kernel utilization distributions (UD) of space-sharing northern spotted owls (SPOW) and barred owls (BAOW) during the breeding (1 Mar–31 Aug) and nonbreeding (1 Sep–28 Feb) seasons in western Oregon, USA, 2007–2009. Overlap combinations included paired females and males (F:M), conspecific neighbors (BAOW:BAOW, SPOW:SPOW), and heterospecific neighbors (BAOW:SPOW) in adjacent nesting territories. Values range from 0 (no overlap) to 1 (100% overlap) except in cases where the 2 UD's have an unusually high degree of overlap, in which case the value is >1 . Box plots bound the 25th and 75th percentiles of the overlap statistic, solid lines within boxes indicate the medians, and whiskers extend to 1.5 times the interquartile range of the observations. Dots indicate extreme values.

greater than what was generally available to owls in the study area (old conifer = 0.17, hardwood = 0.05; Table 5).

Probabilistic measures of spatial overlap that accounted for differences in the intensity of use within the overlap region between 2 neighboring owls indicated that the probability of locating a spotted owl within a barred owl's home range during the breeding season was lower (PHR: $\bar{x}$ = 0.15, SE = 0.03, range = 0.00–0.84) than the probability of locating a barred owl in a spotted owl's home range (PHR: $\bar{x}$ = 0.39, SE = 0.04, range = 0.01–1.00). This directional pattern of interspecific overlap was consistent over all time periods at both levels of use intensity within the home range (Table 7). Estimates of space-use sharing (UDOI) between the species during the breeding season were greater ($\bar{x}$ = 0.10, SE = 0.02, range = <0.01–0.84) than intraspecific estimates for barred owls in adjacent territories ($\bar{x}$ = 0.01, SE = 0.01, range = <0.01–0.02; Fig. 5). This pattern would be expected if barred owls were more likely to share their foraging areas with spotted owls than with other barred owls in adjacent territories. We did not observe a significant increase in interspecific overlap during the nonbreeding season despite the tendency for both species to expand their use of space during this time. We found several cases in 2008 in which the level of space

sharing between individual spotted and barred owls was markedly high (UDOI > 0.30). These were cases in which newly colonizing barred owls were captured and radio-marked within the core-use areas of 2 different pairs of spotted owls (e.g., Fig. 6). Subsequent monitoring indicated a high probability of locating colonizing barred owls within breeding season home ranges (PHR range = 0.55–1.00) and core-use areas (PHR range = 0.52–0.76) of paired male and female spotted owls. Moreover, interspecific territorial interactions were regularly observed in these cases, including agitated vocalizations by both species near nest sites and barred owls physically chasing spotted owls out of shared core-use areas. These observations provided evidence that high interspecific overlap of home ranges and core-use areas was associated with agonistic interactions between the species.

Habitat Use

After excluding owls that died early in the study period and those that spent much of their time beyond the extent of the study area, 25 spotted owls (13 F, 12 M) and 26 barred owls (12 F, 14 M) had sufficient data for analyses of habitat use. For discrete-choice models of nighttime resource selection, we monitored 17 individuals of each species for >1 year, so we developed 2

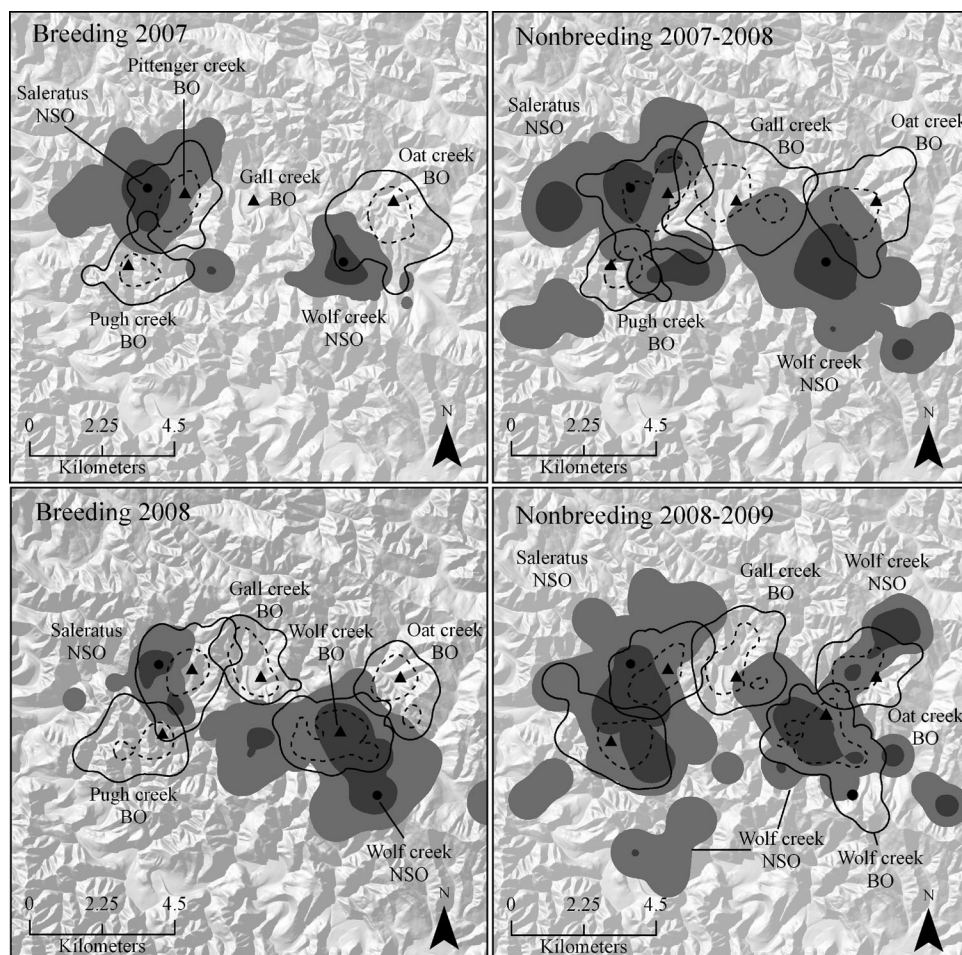


Figure 6. Example of spatial overlap among 2 pairs of northern spotted owls (NSO) and 5 pairs of barred owls (BO) radio-marked in western Oregon, USA, from March 2007 to August 2009. The 95% fixed-kernel home ranges and core-use areas of spotted and barred owls are indicated by shaded and open polygons, respectively. We also show the current year's nest location or breeding season activity center for each pair of spotted owls (dots) and barred owls (triangles). Note change in location of the activity center for the Wolf creek spotted owl pair before (2007) and after the arrival of the Wolf creek barred owl pair in early spring of 2008.

Table 8. Mean values of environmental conditions measured at foraging and roosting locations used by individual northern spotted owls or barred owls as compared to a set of random locations plotted in the western Oregon study area, USA, 2007–2009. Forest types are expressed as the mean percentage of total foraging, roosting, or random locations. We show sample sizes (number of individual owls or random points) in parentheses.

Environmental condition	Spotted owl				Barred owl				Random (<i>n</i> = 11, 974)	
	Foraging (<i>n</i> = 25)		Roosting (<i>n</i> = 16)		Foraging (<i>n</i> = 26)		Roosting (<i>n</i> = 22)			
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Forest type										
Old conifer (%)	38.3	3.2	60.0	3.2	35.0	3.8	41.1	4.4	16.2	0.8
Mature conifer (%)	28.9	3.2	21.9	3.7	23.2	2.9	19.3	3.0	20.9	0.8
Young conifer (%)	17.8	1.6	11.5	1.3	21.9	2.0	22.2	2.1	34.9	0.7
Riparian/hardwood (%)	10.0	1.9	3.8	1.1	15.7	3.0	13.8	3.6	5.4	0.9
Nonforest (%)	5.0	0.6	2.9	1.1	4.2	0.9	3.7	0.9	22.7	0.8
Quadratic mean diameter of conifers (cm)	44.3	1.3	49.7	0.6	42.6	1.8	44.8	0.6	32.4	0.2
Density of conifers >50 cm dbh (no./ha)	17.0	0.6	20.1	0.4	15.4	0.7	16.4	0.3	10.9	0.1
Canopy cover of hardwoods (%)	20.7	0.7	19.7	0.2	19.0	0.8	18.5	0.2	19.2	0.1
Basal area of hardwoods (m ² /ha)	5.4	0.2	5.0	0.1	4.7	0.2	4.6	0.1	5.0	0.1
Slope (degrees)	46.6	1.3	50.1	0.6	39.7	1.7	41.4	0.6	44.3	0.2
Distance to high contrast edge (m)	470.3	49.3	478.3	16.3	500.0	56.5	535.4	13.8	401.1	4.9
Distance to stream (m)	387.3	18.8	398.2	11.6	360.4	37.9	374.1	10.7	453.1	3.2
Distance to nest (m)	2,879.1	428.5	2,868.1	159.3	963.0	71.1	831.3	34.0	3,674.0	42.7

annual choice sets for each of these owls. This process resulted in 42 choice sets for 25 spotted owls (2,820 used locations, 9,209 random locations) and 43 choice sets for 26 barred owls (2,799 used locations, 9,388 random locations). Sixteen spotted owls and 22 barred owls had sufficient data for the univariate analysis of daytime habitat use.

Influence of forest conditions and topography.—Within the extent of the study area (second-order selection), the 2 species displayed broadly similar patterns of habitat use (Table 8). Mean selection ratios indicated that both species used patches of old (>120 yr) conifer forest in proportions 2–3 times greater than their occurrence in the study area (Fig. 7). Based on overlap of 95% Bonferroni confidence intervals, use of old forest for foraging was similar for the 2 species, but spotted owls used old forest in greater proportions for roosting ($\hat{w}_i = 3.74$, 95% CI = 3.23–4.25) than barred owls ($\hat{w}_i = 2.49$, 95% CI = 1.79–3.19). Barred owls used hardwood forest in greater proportions than expected, especially for foraging ($\hat{w}_i = 2.96$, 95% CI = 1.39–4.54). In contrast, spotted owls used hardwood forest in similar proportions to its occurrence. Both species used patches of mature conifer forest in proportions equal to random expectations, and both species were located in patches of young forest and open areas less than expected based on occurrence. Both species used foraging and roosting locations at intermediate distances from high-contrast edges, with selection ratios and confidence intervals being negative for distances <135 m from edges and positive for distances of 490–800 m from edges (Fig. 7). The 2 species also had selection ratios and confidence intervals that were >1.0 for locations ≤150 m from streams. Relative to random locations in the study area, both species were most commonly located in patches of forest characterized by trees with greater average quadratic mean diameter (42–60 cm) and a greater density of conifers >50 cm dbh (15–25 trees/ha; Table 8). Based on Pianka’s measure of niche overlap estimated for 24 pairwise combinations of neighboring spotted and barred owls (48 individuals), mean interspecific similarity in proportional use of different forest types for foraging was 0.809 (SE = 0.022, range = 0.306–0.990). This index indicated a moderate to high level of overlap in use of available forest types by the 2 species.

At the home-range scale (third-order selection), the most strongly supported model of nighttime habitat use for spotted owls without interspecific covariates included the effects of forest type, distance to nest, slope, and distance to streams (Table 9).

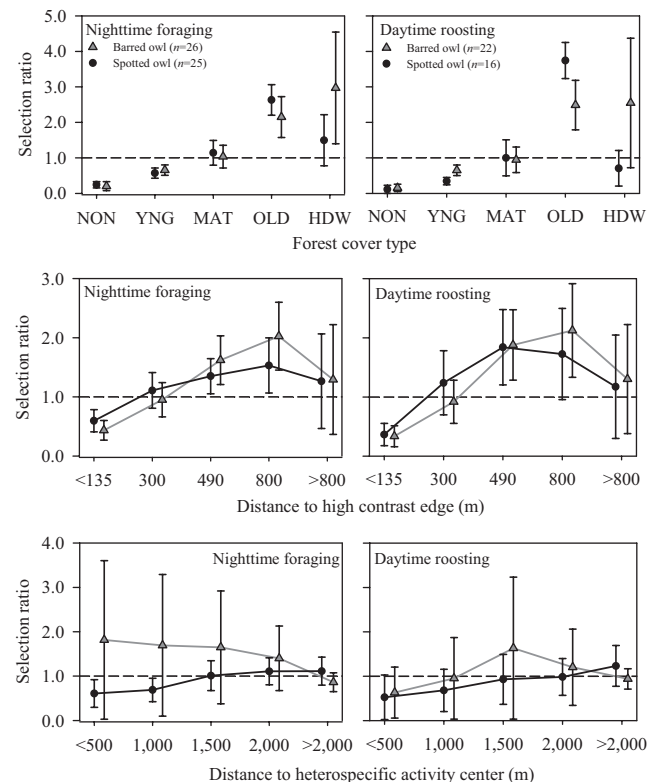


Figure 7. Mean selection ratios and 95% Bonferroni confidence intervals illustrating the influence of forest type, high contrast edges, and the distribution of heterospecific activity centers on use of foraging and roosting locations by sympatric northern spotted owls and barred owls in western Oregon, USA, 2007–2009. The dashed horizontal line indicates the level at which use is equal to occurrence in the study area (second-order selection); values with confidence intervals >1 indicate that use is greater than expected based on occurrence, values with confidence intervals <1 indicate that use is less than expected based on occurrence. Forest types were nonforest (NON), young conifer (YNG), mature conifer (MAT), old conifer (OLD), and riparian-hardwood (HWD).

Table 9. Ranking of top 5 discrete-choice models used to characterize nighttime habitat use within home ranges of sympatric northern spotted owls and barred owls in western Oregon, USA, 2007–2009. We also show the null model without explanatory covariates for comparisons.

Species and model ^a	<i>K</i>	$-2\log L$	AIC	Δ AIC	AIC wt
Spotted owl (<i>n</i> = 25 owls, 42 choice sets)					
Fortype + dnest ² + slope + dstream + dHET + (HDW × dHET)	10	30,994.2	31,014.2	0.00	0.90
Fortype + dnest ² + slope + dstream + dHET	9	31,001.8	31,019.8	5.53	0.06
Fortype + dnest ² + slope + dstream + dHET + (OLD × dHET)	10	31,000.4	31,020.4	6.14	0.04
Fortype + dnest ² + slope + dstream + HETcore	9	31,013.3	31,031.3	17.07	0.00
Fortype + dnest ² + slope + dstream	8	31,029.6	31,045.6	31.38	0.00
Null model (no effects)	0	31,964.5	31,964.5	950.31	0.00
Barred owl (<i>n</i> = 26 owls, 43 choice sets)					
Fortype + dnest ² + slope + dedge ² + dstream	10	30,653.3	30,673.3	0.00	0.41
Fortype + dnest ² + slope + dedge ² + dstream + dHET + (OLD × dHET)	12	30,651.0	30,675.0	1.72	0.17
Fortype + dnest ² + slope + dedge ² + dstream + HETcore	11	30,653.2	30,675.2	1.96	0.15
Fortype + dnest ² + slope + dedge ² + dstream + dHET	11	30,653.3	30,675.8	2.55	0.12
Fortype + dnest ² + slope + dedge ² + dstream + dHET + (HDW × dHET)	12	30,652.5	30,676.5	3.23	0.08
Null model (no effects)	0	31,625.4	31,625.4	952.16	0.00

^a Key to model notation: *K* = number of covariates in the model; $-2\log L$ = value of the maximized log-likelihood function; Δ AIC = difference between the AIC value of each model and the lowest AIC model; AIC wt = Akaike weight; fortype = forest type, a categorical variable with 5 levels: old conifer (OLD), mature conifer (MAT), young conifer (YNG), riparian/hardwood (HDW), and nonforest (NON). Other model covariates included slope, distance to nest (dnest), distance to stream (dstream), distance to high contrast edge (dedge), proximity to heterospecific core-use area (dHET), and area within a heterospecific neighbor's core-use area (HETcore).

A competing model without interspecific covariates (Δ AIC = 0.55; Appendix E) included a quadratic term for distance to high-contrast edge, but the 95% confidence interval for this effect narrowly included 0 ($\hat{\beta}$ = 0.18, SE = 0.14, 95% CI = −0.10 to 0.46), which provided some evidence that spotted owls foraged away from forest edges. Our best model for spotted owls indicated that old conifer was >5 times as likely to be used for foraging as the nonforest reference category (selection ratio [$\exp(\hat{\beta})$] = 5.3, 95% CI = 4.4–6.4), followed by riparian-hardwood (4.3, 95% CI = 3.5–5.4), mature conifer (3.4, 95% CI = 2.8–4.1), and young conifer forest (1.9, 95% CI = 1.6–2.4). This model also indicated a positive association between resource use and steeper slopes by spotted owls, and that the

relative probability of use declined as distance from nest sites and streams increased.

Similar to spotted owls, the most strongly supported model of nighttime habitat use for barred owls included the effects of forest type, slope, distance to nest, and distance to streams (Table 9). In contrast to spotted owls, however, barred owls used steep slopes less than expected (Table 10). We also found stronger support for a quadratic effect of high-contrast edges on resource use by barred owls as compared to spotted owls. Our best model for barred owls indicated that riparian-hardwood forest was >3 times as likely to be used for foraging as the nonforest reference (selection ratio = 3.2, 95% CI = 2.5–4.0), followed by old conifer (2.9, 95% CI = 2.3–3.5), mature conifer (2.6, 95% CI = 2.1–3.1), and then

Table 10. Parameter estimates ($\hat{\beta}$) from the best discrete-choice resource selection functions developed separately for sympatric northern spotted owls and barred owls in western Oregon, USA, 2007–2009. The reference level for forest type was nonforest.

Covariate	$\hat{\beta}$	SE	Approximate 95% CI ^a	
			Lower	Upper
Spotted owls				
Old conifer	1.694	0.095	1.508	1.881
Mature conifer	1.210	0.095	1.024	1.397
Young conifer	0.697	0.098	0.506	0.889
Riparian-hardwood	1.618	0.121	1.380	1.856
Distance to nest (km)	−0.140	0.015	−0.168	−0.111
Distance to nest ² (km)	0.004	0.001	0.003	0.006
Slope (degrees)	0.002	0.001	0.000	0.005
Distance to stream (km)	−0.489	0.064	−0.615	−0.362
Proximity to barred owl (km)	0.100	0.018	0.065	0.134
Riparian-hardwood × proximity to barred owl	−0.100	0.042	−0.181	−0.018
Barred owls				
Old conifer	1.050	0.108	0.837	1.262
Mature conifer	0.938	0.106	0.729	1.147
Young conifer	0.516	0.109	0.302	0.729
Riparian-hardwood	1.155	0.115	0.930	1.380
Distance to nest (km)	−0.808	0.045	−0.897	−0.720
Distance to nest ² (km)	0.070	0.006	0.059	0.081
Slope (degrees)	−0.006	0.001	−0.009	−0.004
Distance to edge (km)	0.454	0.159	0.142	0.766
Distance to edge ² (km)	−0.226	0.098	−0.419	−0.033
Distance to stream (km)	−0.222	0.079	−0.377	−0.067

^a Approximate 95% confidence interval calculated as: coefficient ± 1.96(coefficient SE).

young conifer forest (1.7, 95% CI = 1.4–2.1). Thus, similar to results from broader spatial scales, barred owls showed a more even distribution of use of available forest types within their home ranges than spotted owls. Discrete-choice models that included forest structural conditions were not competitive with those containing the categorical effect of forest type (Appendix E). Nonetheless, we found some support for a nonlinear effect of average quadratic mean diameter of conifers (QMD) on use of foraging sites by both species, as indicated by 95% confidence intervals that did not overlap 0. Models including this effect indicated that use was maximized in forest patches with average QMD of 40–65 cm for both species.

When data from both species were combined, the best model of differential habitat use was the most complex structure with all interactions between species and explanatory covariates (AIC weight = 1.0; Appendix E, Fig. 8). This model was >257 AIC units less than a model without species effects, which provided strong evidence of differential use of foraging conditions by spotted owls and barred owls. Covariates included in the best model for both species combined were the same as those included in our best model for barred owls, which meant that parameter estimates under the combined model (where barred owls were the reference level; Table 11) matched those estimated under the best-supported barred owl model (Table 10). As indicated by parameter coefficients and 95% confidence intervals for species interaction terms, the 2 species differed most in the relative use of slope conditions (steeper slopes for spotted owls), old conifer forest (greater for spotted owls), and distance to nest (closer distances for barred owls; Fig. 8). We found no evidence that the 2 species differed in their use of young, mature, or riparian-hardwood forest types (Table 11).

Influence of heterospecifics.—Spotted owls used locations within 1,000 m of known territory centers of barred owls less than

expected based on occurrence in the study area ($\hat{w}_i = 0.61$, 95% CI = 0.30–0.92 for distances <500 m; $\hat{w}_i = 0.69$, 95% CI = 0.42–0.95 for distances of 500–1,000 m; Fig. 7). Foraging locations of barred owls were closer to areas used by spotted owls ($\bar{x} = 2.7$ km, SE = 0.3 km) than to random locations ($\bar{x} = 3.8$ km, SE = 0.2 km), but proportional use of different distance classes surrounding spotted owl activity centers did not deviate significantly from random expectations. This result was due in part to the sparse distribution of spotted owls in our study area, which likely contributed to a high level of variation among individual barred owls in their exposure to spotted owls.

At the home-range scale of analysis, spatial covariates representing areas of concentrated use by barred owls contributed further in explaining variation in habitat use by spotted owls; discrete-choice models with covariates representing core-use areas of barred owls (HETcore) or proximity to a barred owl core-use area (dHET) were 14.3–31.4 AIC units less than the best model without these effects (Table 9). Parameter coefficients for the effect of HETcore showed that the relative probability of a spotted owl using a location at night was significantly reduced if the location was within a core-use area of barred owls (discrete-choice selection ratio = 0.72, 95% CI = 0.61–0.85). The overall best model of resource use for spotted owls, however, included the effect of proximity to barred owls plus an interaction between riparian-hardwood forest and proximity to barred owls (Table 9). This model accounted for 90% of the AIC weight and indicated that use of different forest types varied with increasing proximity to barred owls. As proximity to a barred owl's core-use area increased, a spotted owl's affinity for old, mature, and young conifer forest types was gradually replaced by use of riparian-hardwood forest (Fig. 9). For barred owls, inclusion of variables representing spatial overlap with spotted owls failed to improve upon models without these effects (Table 9), and the 95%

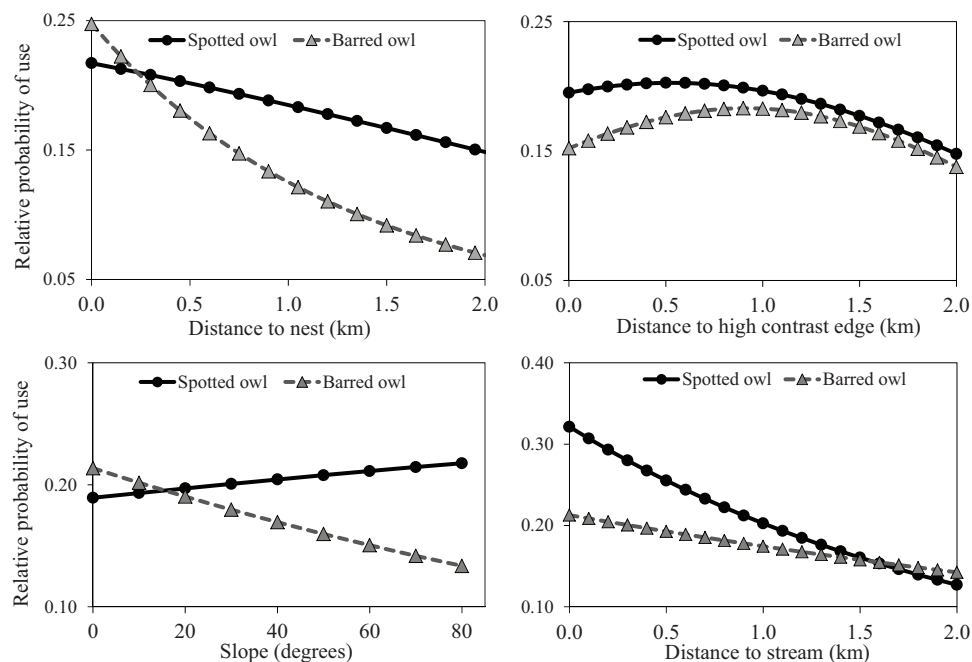


Figure 8. Relative probability of use as a function of covariates included in the best discrete choice model of differential habitat use within home ranges of sympatric northern spotted owls and barred owls in western Oregon, USA, 2007–2009. We show predicted values for the old conifer forest type; variables not plotted were held constant at their median values.

Table 11. Parameter estimates ($\hat{\beta}$) from the best model of differential habitat use by sympatric northern spotted owls and barred owls in western Oregon, USA, 2007–2009. The reference level for forest type was nonforest and the reference level for species was barred owl.

Covariate	$\hat{\beta}$	SE	Approximate 95% CI ^a	
			Lower	Upper
Old conifer (OLD)	1.050	0.108	0.837	1.262
Mature conifer (MAT)	0.938	0.106	0.729	1.147
Young conifer (YNG)	0.516	0.109	0.302	0.729
Riparian-hardwood (HDW)	1.155	0.115	0.930	1.380
Distance to nest (km)	−0.808	0.045	−0.897	−0.720
Distance to nest ² (km)	0.070	0.006	0.059	0.081
Slope (degrees)	−0.006	0.001	−0.009	−0.004
Distance to edge (km)	0.454	0.159	0.142	0.766
Distance to edge ² (km)	−0.226	0.098	−0.419	−0.033
Distance to stream (km)	−0.222	0.078	−0.376	−0.069
Species-specific interactions				
Species × OLD	0.598	0.147	0.309	0.887
Species × MAT	0.264	0.146	−0.023	0.551
Species × YNG	0.150	0.150	−0.144	0.444
Species × HDW	0.294	0.162	−0.023	0.611
Species × dnest	0.664	0.048	0.571	0.757
Species × dnest ²	−0.063	0.006	−0.074	−0.052
Species × slope	0.009	0.002	0.005	0.012
Species × dedge	−0.301	0.215	−0.722	0.119
Species × dedge ²	0.093	0.131	−0.163	0.350
Species × dstream	−0.265	0.102	−0.465	−0.065

^a Approximate 95% confidence interval calculated as: coefficient $\pm$ 1.96 (coefficient SE).

confidence intervals for effects of spotted owls on barred owls broadly overlapped 0. Consequently, we found little evidence that the presence of spotted owls influenced habitat use by barred owls.

Diets and Foraging Behavior

We identified 1,223 prey items from 15 territories occupied by spotted owls and 4,299 prey items from 24 territories occupied by barred owls. The number of prey items from each territory ranged from 20 to 173 for spotted owls ($\bar{x}$ = 81.5, SE = 11.8) and 28 to 441 for barred owls ($\bar{x}$ = 179.1, SE = 26.2). Diets of spotted and

barred owls included at least 51 and 95 prey species, respectively (Appendix F). The diet of spotted owls was dominated by mammals, which composed an average of 95.7% of total prey numbers and 97.4% of total prey biomass (Table 12). In comparison, mammals composed 66.0% of prey numbers and 89.2% of prey biomass in diets of barred owls, with the remainder being composed of birds, frogs, salamanders, lizards, snakes, crayfish, snails, fish, millipedes, and insects. We found no evidence of intraguild predation between the 2 species based on the absence of spotted or barred owl remains in diet samples.

Based on percent biomass contributions to diets, the 5 main prey species for spotted owls were (in descending order): northern flying squirrels (50.0%), woodrats (17.4%), lagomorphs (13.3%), deer mice (*Peromyscus maniculatus*; 4.9%), and red tree voles (*Arborimus longicaudus*; 4.4%). In comparison, the 5 main prey for barred owls were: northern flying squirrels (24.3%), lagomorphs (17.4%), moles (14.8%), Douglas squirrels (*Tamiasciurus douglasii*; 6.9%), and woodrats (6.8%). Thus, flying squirrels, woodrats, and lagomorphs were primary prey for both owl species, accounting for 80.7% and 48.5% of total dietary biomass for spotted owls and barred owls, respectively. No single bird species accounted for >2.0% of dietary biomass for either species.

The majority of prey consumed by both species were nocturnal, but barred owls also consumed a high frequency of diurnal prey (e.g., squirrels, birds, reptiles) that were rare or absent in diets of spotted owls ($\chi^2_3 = 324.7$, $P < 0.001$; Fig. 10). Both owls fed upon similar proportions of semi-arboreal species, but within this prey group, spotted owls fed more heavily on nocturnal woodrats and barred owls fed more heavily on diurnal squirrels. Diets of spotted owls contained a greater frequency of arboreal prey (e.g., flying squirrels, red tree voles) than those of barred owls ($\chi^2_6 = 827.37$, $P < 0.001$). Conversely, barred owl diets contained a greater frequency of prey associated with terrestrial and aquatic environments (Fig. 10).

Mean FNB was 4.44 for spotted owls (SE = 0.25, range = 2.11–6.12, n = 15 territories) and 8.40 for barred owls (SE = 0.39, range = 3.63–12.40, n = 24 territories). Standardized measures of FNB confirmed that diets of barred owls were considerably more diverse (FNBst = 0.26, SE = 0.01) than those of spotted owls (FNBst = 0.12, SE = 0.01). This result was supported by the rarefaction analysis, which illustrated that diets of barred owls consistently contained a greater richness of prey than diets of spotted owls over a range of simulated sampling frequencies (Fig. 11). Estimates of dietary breadth for barred owls were greater than spotted owls, but values for both species were near the lower end of the scale of possible values (1–30), which suggested that use of different prey types was uneven.

The average size of individual prey captured by barred owls was smaller than prey captured by spotted owls. When insects were included, mean mass of prey was 91.0 g for spotted owls (SE = 6.2, 95% CI = 77.7–104.2) and 60.2 g for barred owls (SE = 3.1, 95% CI = 53.7–66.6). Mean mass of noninsect prey was 92.5 g for spotted owls (SE = 6.4, 95% CI = 78.8–106.1) and 68.8 g for barred owls (SE = 3.0, 95% CI = 62.7–74.9 g). Both species captured prey in a variety of sizes ranging from hymenopteran bees (0.1 g) to adult snowshoe hares (approx. 1,200 g). Diets of spotted owls, however, were dominated by prey in the 11–40 g and 81–160 g size classes, whereas diets of barred

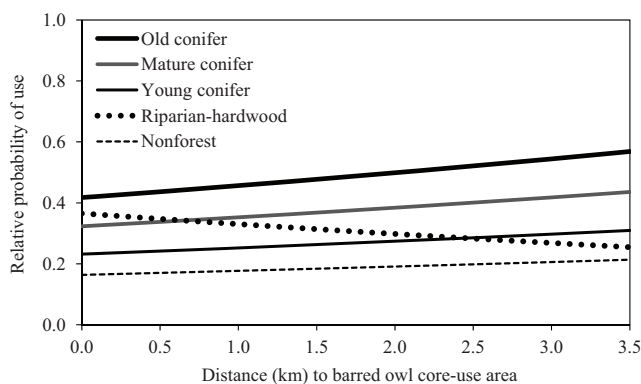


Figure 9. Relative probability of a location being used at night by a northern spotted owl as a function of forest type and proximity to the nearest barred owl core-use area in western Oregon, USA, 2007–2009. Predicted values are from the best discrete choice model of habitat use for spotted owls, which included an interaction between the riparian-hardwood forest type and distance to nearest core-use area of a barred owl. Covariates not plotted were held constant at their median values.

Table 12. Dietary composition of sympatric northern spotted owls and barred owls in western Oregon, USA, 2007–2009. Diets are expressed as the mean percent of the total number and total biomass of prey identified in owl pellets from pairs of spotted owls or barred owls. Sample sizes (number of owl pairs with >20 prey items) are in parentheses.

Prey species ^c	% of prey numbers ^a				% of prey biomass ^b			
	Spotted owl (n = 16)		Barred owl (n = 25)		Spotted owl (n = 16)		Barred owl (n = 25)	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Mammals	95.7	1.1	66.0	2.9	97.4	0.7	89.2	1.2
Northern flying squirrel (<i>Glaucomys sabrinus</i>)	37.8	3.4	11.6	1.2	50.0	3.3	24.3	1.8
Deer mouse (<i>Peromyscus maniculatus</i>)	17.3	2.6	3.5	0.6	4.9	1.0	1.3	0.2
Red tree vole (<i>Arborimus longicaudus</i>)	14.7	2.2	3.4	0.6	4.6	0.8	1.5	0.3
Woodrat (<i>Neotoma fuscipes</i> , <i>N. cinerea</i>)	8.1	1.4	1.5	0.3	17.4	2.5	6.8	1.3
Unidentified vole or mouse (<i>Muridae</i> spp.)	4.0	0.9	0.3	0.1	1.0	0.3	0.1	0.0
Rabbits, hares (<i>Sylvilagus bachmani</i> , <i>Lepus americanus</i>)	3.4	0.6	2.5	0.4	13.3	2.5	17.4	3.0
Western red-backed vole (<i>Myodes californicus</i>)	2.8	0.8	1.3	0.3	0.9	0.3	0.5	0.1
Shrews, shrew-moles (<i>Sorex</i> spp., <i>Neurotrichus gibbsii</i>)	1.9	0.9	13.8	0.9	0.2	0.1	1.4	0.1
Mountain beaver (<i>Aplodontia rufa</i>)	0.9	0.4	1.0	0.3	1.9	0.7	5.5	1.5
Other voles (<i>Microtus</i> spp.)	0.9	0.3	2.0	0.4	0.3	0.1	1.1	0.3
Moles (<i>Scapanus orarius</i> , <i>S. townsendii</i>)	0.8	0.3	17.9	1.5	0.2	0.1	14.8	1.7
Douglas squirrel (<i>Tamiasciurus douglasii</i>)	0.8	0.3	2.0	0.3	1.4	0.5	6.9	0.8
Western pocket gopher (<i>Thomomys mazama</i>)	0.7	0.3	0.3	0.1	0.9	0.5	0.5	0.2
Townsend's chipmunk (<i>Tamias townsendii</i>)	0.5	0.2	1.2	0.3	0.3	0.2	1.7	0.5
Pacific jumping mouse (<i>Zapus trinotatus</i>)	0.4	0.2	0.7	0.2	0.1	0.1	0.3	0.1
Bats (<i>Eptesicus fuscus</i> , <i>Myotis</i> spp.)	0.3	0.1	0.3	0.2	<0.1	0.0	<0.1	0.0
Ermine (<i>Mustela erminea</i>)	0.3	0.2	0.2	0.1	0.1	0.1	0.2	0.1
Western gray squirrel (<i>Sciurus griseus</i>)			0.1	0.1			0.3	0.2
Western spotted skunk (<i>Spilogale gracilis</i>)			0.4	0.2			2.8	1.5
Black rat (<i>Rattus rattus</i>)			<0.1	0.0			0.2	0.2
Common muskrat (<i>Ondatra zibethicus</i>)			<0.1	0.0			0.7	0.7
Unidentified weasel (<i>Mustela</i> spp.)			1.6	0.3			0.8	0.2
Birds	3.1	0.6	2.8	0.3	3.1	0.6	4.3	0.9
Amphibians	0.1	0.1	8.0	0.9	0.1	0.1	2.8	0.3
Salamanders	0.1	0.1	7.0	0.7	0.1	0.1	2.5	0.4
Frogs (<i>Rana</i> spp.)			1.0	0.6			0.4	0.1
Reptiles	0.0	0.0	1.1	0.3	0.0	0.0	1.5	0.4
Insects, millipedes, and springtails	1.0	0.5	12.5	2.0	0.0	0.0	0.1	0.0
Signal crayfish (<i>Pacifastacus leniusculus</i>)	0.1	0.1	2.6	1.3	<0.1	0.0	1.1	0.7
Snails	0.2	0.1	6.9	1.8	<0.1	0.0	0.7	0.1
Fish (small salmonids)			0.2	0.1			0.2	0.1

^a Total number of prey items was 1,238 for spotted owls and 4,299 for barred owls.

^b Total prey biomass was 112,661 g for spotted owls and 258,598 g for barred owls.

^c See Appendix F for a complete list of prey species identified in owl diets.

owls were more evenly distributed among prey-sizes (Fig. 12). Unlike spotted owls, barred owls consumed a large proportion of very small (≤ 10 g) prey that included at least 14 species of insects, 4 species of snails, 4 species of shrews, and 5 species of small birds (Appendix F). Barred owls also took a disproportionately greater number of prey items within the 41–80-g size range, including coast moles (*Scapanus orarius*), Townsend's chipmunks (*Tamias townsendii*), and large salamanders (*Ambystoma* or *Dicamptodon* spp.).

Mean dietary overlap between pairs of spotted owls and barred owls in adjacent territories was 0.42 (SE = 0.03, range = 0.28–0.70; Table 13). Mean overlap in the proportional use of mammals was 0.51 (SE = 0.03, range = 0.34–0.73). Estimates of interspecific overlap from null model simulations were less than those observed (range = 0.14–0.27; Table 13), indicating that the level of dietary overlap we observed was greater than what would be expected if proportional use of prey types was random. Based on data pooled over all territories, dietary overlap increased from 0.45 during the breeding season to 0.68 in the nonbreeding season. In the latter season, amphibians, reptiles, crayfish, and insects were less available and both species were more strongly restricted to mammalian prey. Proportional use of mammals by

spotted owls was similar during breeding (94.1%) and nonbreeding (95.6%) periods. In contrast, the frequency of mammals in the diet of barred owls increased from 63.5% in the breeding season to 71.3% in the nonbreeding season with a concomitant increase in the mean mass of prey captured (Table 14). Seasonal changes in diets of barred owls were most strongly related to increases in the proportional use of flying squirrels, red tree voles, and lagomorphs during fall and winter.

Trophic and Ecological Overlap

A comparison of mean overlap coefficients estimated for each of the 3 resource dimensions showed that neighboring spotted owls and barred owls were most similar in their use of primary forest types ($\bar{x} = 0.81$, SE = 0.04), followed by diets ($\bar{x} = 0.43$, SE = 0.02) and spatial distributions ($\bar{x} = 0.17$, SE = 0.04; Table 15). Trophic overlap estimated for neighboring spotted and barred owls ranged from 0.09 to 0.50 ($\bar{x} = 0.35$, SE = 0.02; Table 15), indicating that interspecific similarities in the collective use of available forest types and prey varied considerably among individuals in adjacent territories. Ecological overlap based on the arithmetic mean of space, habitat, and dietary overlap coefficients also varied widely among individuals, ranging from

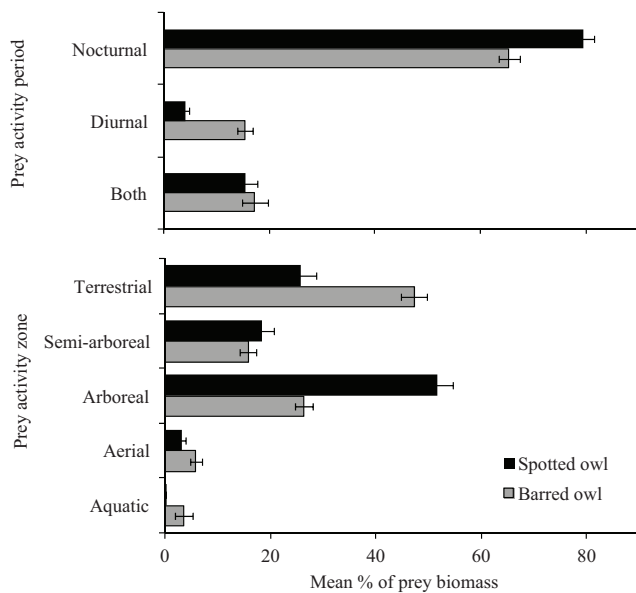


Figure 10. Diets (mean percent of prey biomass per territory $\pm$ SE) of northern spotted owls and barred owls in western Oregon, USA, 2007–2009, categorized by the primary activity period and activity zone of prey species identified in owl pellets. We estimated diets from pellets collected at 15 and 24 territories occupied by spotted and barred owls, respectively.

0.23 to 0.69 ($\bar{x}$ = 0.47, SE = 0.02). We likely underestimated measures of trophic and ecological overlap because estimates did not account for cumulative overlap among all heterospecific neighbors or for potential seasonal or annual variation in prey availability.

Survival and Reproduction

Causes of death and survival probabilities.—We documented 13 fatalities of radio-marked owls (9 spotted owls, 4 barred owls; Table 16). Nine carcasses (5 spotted owls, 4 barred owls) were recovered fully intact and submitted for necropsy. Necropsy results showed no injuries directly attributable to radio transmitters, and all owls tested negative for West Nile Virus

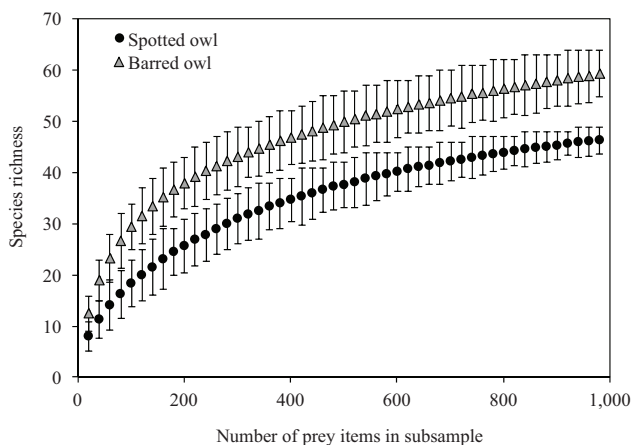


Figure 11. Rarefaction curves illustrating differences in expected number of prey species captured by northern spotted owls and barred owls over a range of simulated sample sizes. We estimated point estimates and 95% confidence intervals from 2,000 repeated randomizations of observed diets in western Oregon, USA, 2007–2009.

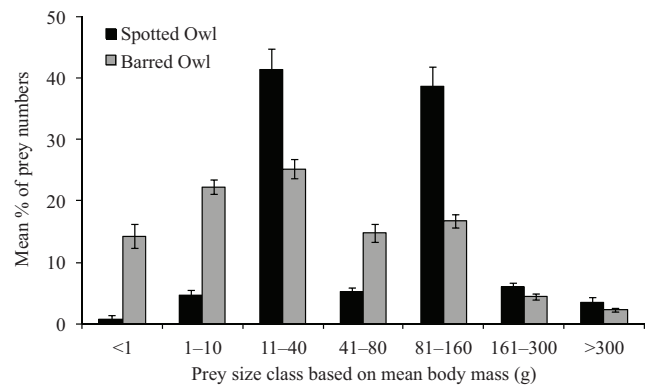


Figure 12. Dietary overlap between neighboring pairs of northern spotted owls (n = 15) and barred owls (n = 24) in western Oregon, USA, 2007–2009, based on the mean percentage ($\pm$ SE) of prey captured in different size classes.

(*Flavivirus*). Based on necropsy results and evidence collected at recovery sites, causes of death included severe bacterial infections associated with endoparasitism (6 cases), disease (1 case), emaciation (1 case), and avian predation (5 cases). Avian predation was identified as the primary cause of death in spotted owls (56%; 5 of 9 cases), whereas severe bacterial infection associated with heavy infestations of parasitic worms (e.g., *Acanthocephala* spp.) was the primary cause of death in barred owls. One male spotted owl was found dead of emaciation just 9 days after the death of his mate, who died of a possible pneumonia infection shortly after a failed nesting attempt. We found no evidence that predation was a factor in the death of barred owls. The remains of 2 spotted owls were located (in different years) at a perch where great horned owls had been observed. In both cases, we found the radio transmitter along with scattered feathers, whitewash, and large owl pellets containing remains of the spotted owls. The other 2 spotted owls were found partially eaten and cached beneath fallen logs shortly after their fatality sensors activated. These owls had wounds consistent with those inflicted by a large avian predator and were recovered in areas where both great horned owls and barred owls were detected. Although we could not rule out the possibility that barred owls were responsible for these deaths, we found no evidence to support this cause.

We partitioned survival of radio-marked spotted owls and barred owls by 6-month time intervals to provide estimates of seasonal, annual, and cumulative survival probabilities over a 22-month period (May 2007–Feb 2009). The number of individuals of each species included in each 6-month time interval ranged from 21 to 26 (Table 16). We did not censor any owls because we knew the fate of all owls perfectly (no emigration or unexplained loss of signals), and no radio transmitters failed during the time intervals in which we estimated survival. Consequently, our estimates of survival were free of bias due to the confounding of mortality with transmitter failure or emigration. The most strongly supported model without habitat or interspecific covariates, $S(Spp)$, indicated that survival differed between species (higher for barred owls) and was constant between sexes and over time (Table 17). The 95% confidence interval for the effect of species in this model narrowly included 0 (β = -0.92 , SE = 0.62, 95% CI = -2.14 to 0.30), indicating weak support for species-specific differences in survival. The derived estimate of

Table 13. Observed versus simulated estimates of dietary overlap between neighboring pairs of northern spotted owls and barred owls in western Oregon, USA, 2007–2009.

Pair ID	No. prey items ^a		Observed dietary overlap ^b	Mean of simulated overlaps (SE) ^b	<i>P</i> ^c
	Spotted owl	Barred owl			
1	67	94	0.411	0.220 (0.020)	0.106
2	146	439	0.505	0.188 (0.022)	0.032
3	32	90	0.411	0.169 (0.023)	0.086
4	72	352	0.277	0.191 (0.022)	0.175
5	110	439	0.393	0.156 (0.021)	0.077
6	42	215	0.392	0.143 (0.022)	0.122
7	173	274	0.470	0.237 (0.018)	0.070
8	59	185	0.380	0.266 (0.019)	0.179
9	56	90	0.472	0.203 (0.019)	0.056
10	94	94	0.312	0.223 (0.021)	0.218
11	20	65	0.283	0.184 (0.021)	0.242
12	55	378	0.373	0.230 (0.019)	0.178
13	60	255	0.696	0.268 (0.021)	0.005
14	82	57	0.363	0.171 (0.021)	0.087
15	155	171	0.531	0.257 (0.017)	0.059
Mean (SE)	82 (12)	213 (35)	0.418 (0.028)	0.207 (0.010)	

^a Total number of prey items identified in pellets from neighboring pairs of spotted owls and barred owls ($n = 30$ owl pairs total).

^b Pianka's index of niche overlap (Pianka 1973).

^c Probability that the observed value of dietary overlap is greater than or equal to the mean of simulated overlaps generated from 2,000 Monte Carlo randomizations of the observed diet data.

annual (12-month) survival under this model was 0.81 for spotted owls (SE = 0.05, 95% CI = 0.68–0.90) and 0.92 for barred owls (SE = 0.04, 95% CI = 0.80–0.97). Models containing the effects of sex, year, or season were not supported by the data (AIC_c wt = 0; Appendix G), and 95% confidence intervals for these effects broadly overlapped 0.

Our best model for survival included the additive effect of species, mean proportion of old conifer forest in the home range, and the probability of heterospecific presence in the home range (Table 17). The slope coefficient for the effect of old forest in this model ($\beta = 10.15$, SE = 3.92, 95% CI = 2.46–17.84) indicated a strong positive relationship with survival of both species. This

model indicated that survival was highest for owls with >45% of old forest in their home range (Fig. 13). Moreover, models that included the effect of old forest consistently outperformed those without this covariate (Table 17, Appendix G). On average, owls that survived had greater proportions of old forest in their home ranges (spotted owls: $\bar{x} = 0.20$, SE = 0.02; barred owls: $\bar{x} = 0.23$, SE = 0.03) than owls that died (spotted owls: $\bar{x} = 0.14$, SE = 0.03; barred owls: $\bar{x} = 0.11$, SE = 0.04). The negative and additive effect of the probability of heterospecific presence in the home range was also included in the top model, but the 95% confidence interval for this effect overlapped 0 slightly ($\beta = -1.98$, SE = 1.35, 95% CI = -4.62 to 0.66), indicating a weak

Table 14. Seasonal changes in diet composition (% of total prey numbers) and mean mass of prey (g) of sympatric northern spotted owls and barred owls in western Oregon, USA, 2007–2009. The breeding season was 1 March–31 August and the nonbreeding season was 1 September–28 February. We also provide numbers of prey items (n).

Prey species	Spotted owl		Barred owl	
	Breeding ($n = 1,156$)	Nonbreeding ($n = 67$)	Breeding ($n = 4,048$)	Nonbreeding ($n = 251$)
Mammals	94.2	95.5	63.5	71.3
Northern flying squirrel	36.5	25.4	11.0	19.1
Deer mouse	18.2	19.4	3.5	2.8
Red tree vole	14.2	18.0	3.5	5.2
Woodrat	7.2	9.0	1.4	2.0
Rabbits, hares	3.8	4.5	1.9	2.8
Shrews, shrew moles	2.1	3.0	13.0	13.6
Moles	0.9	1.5	18.4	8.4
Mountain beaver	0.9	0.0	0.9	0.0
Douglas squirrel	0.9	1.5	2.0	3.6
Other mammals	9.5	13.2	7.9	13.8
Birds	4.0	1.5	3.0	5.6
Amphibians	0.1	0.0	9.3	5.6
Reptiles	0.1	0.0	0.9	0.8
Insects	1.5	1.5	13.0	9.5
Snails	0.1	1.5	6.5	3.2
Fish	0.0	0.0	0.2	1.6
Crayfish	<0.01	0.0	5.7	0.8
Mean mass (g) of prey (SE)	91.3 (3.1)	84.0 (14.2)	59.0 (1.7)	78.8 (6.8)
Interspecific dietary overlap ^a	0.446	0.676	0.446	0.676

^a Pianka's index of food niche overlap (Pianka 1973). We pooled diet data over territories.

Table 15. Trophic and ecological overlap indices for individual northern spotted owls and barred owls that were radio-marked in adjacent territories in western Oregon, USA, 2007–2009.

Spotted owl ID ^a	Barred owl ID ^a	Spatial overlap (S) ^b	Habitat overlap (H) ^c	Dietary overlap (D) ^c	Trophic overlap (H × D)	Ecological overlap (S + H + D)/3
BUL_SF	PAT_BF	0.056	0.877	0.411	0.360	0.448
BUL_SM	PAT_BF	0.163	0.902	0.411	0.371	0.492
CC_SF	EC_BF	0.124	0.905	0.505	0.457	0.511
CC_SM	EC_BM	0.149	0.859	0.505	0.434	0.504
DC_SF	SF_BF	0.094	0.306	0.277	0.085	0.226
DC_SM	SF_BF	0.134	0.575	0.277	0.159	0.329
EC_SF	EC_BF	0.155	0.829	0.393	0.326	0.459
HC_SF	SC_BM	0.102	0.956	0.392	0.375	0.483
HC_SM	SC_BM	0.129	0.925	0.392	0.363	0.482
IM_SF	IM_BF	0.032	0.987	0.470	0.464	0.496
IM_SM	IM_BF	0.107	0.967	0.470	0.454	0.515
LEO_SF	KLI_BF	0.168	0.493	0.380	0.187	0.347
LEO_SM	KLI_BF	0.130	0.736	0.380	0.280	0.415
LM_SF	SG_BM	0.033	0.914	0.472	0.431	0.473
PAT_SM	PAT_BF	0.579	0.795	0.312	0.248	0.562
PAT_SM2	PAT_BF	0.144	0.819	0.312	0.256	0.425
SAL_SF	UPC_BF	0.328	0.846	0.373	0.316	0.516
SAL_SM	UPC_BM	0.702	0.986	0.373	0.368	0.687
SCW_SF	LBC_BF	0.003	0.448	0.696	0.312	0.382
SCW_SM	LBC_BF	0.000	0.509	0.696	0.354	0.402
WC_SF	WC_BF	0.475	0.990	0.363	0.359	0.609
WC_SM	WC_BM	0.361	0.971	0.363	0.352	0.565
WP_SF	HP_BM	0.008	0.873	0.531	0.464	0.471
WP_SM	HP_BM	0.000	0.938	0.531	0.498	0.490
Mean		0.174	0.809	0.429	0.345	0.470
Median		0.130	0.875	0.393	0.360	0.483
SE		(0.037)	(0.039)	(0.022)	(0.021)	(0.019)

^a First 2–3 letters indicate site name, second to last letter indicates species, last letter indicates sex.

^b Estimated as the proportion of a spotted owl's 95% fixed-kernel home range that was overlapped by the home range of the nearest neighboring barred owl.

^c Calculated using Pianka's (1973) measure of niche overlap. Dietary overlap was based on proportional use of 30 prey categories and habitat overlap was based on proportional use of 5 forest cover types. Values of habitat overlap incorporated availability of each forest type in the study area.

but imprecise effect of heterospecific presence on survival. Models containing the effects of high-contrast edges, proportion of old conifer in the breeding season core-use area, and proportion of the home range shared with heterospecific neighbors were not supported by the modeling results and data (Appendix G).

Nesting success and reproductive output.—We found a dramatic difference in annual estimates of nesting success and reproductive output between spotted owls and barred owls (Table 18). In general, pairs of barred owls nested more often, had fewer nest failures, and produced an average of 4.4 times as many young over a 3-year period as pairs of spotted owls did. Over 3 breeding

Table 16. Causes of death and estimates of model-averaged survival probabilities ($\hat{S}$) for radio-marked northern spotted owls and barred owls in western Oregon, USA, 2007–2009.

Time interval and species	Owls at risk	Deaths (females, males)	Cause of death ^a			Survival probability ^b	
			Avian predation	Endoparasitism or bacterial infection	Disease or starvation	$\hat{S}$	$\widehat{SE}$
May–Aug 2007							
Spotted owl	24	1 (0, 1)	1	0	0	0.903	0.040
Barred owl	22	1 (0, 1)	0	1	0	0.947	0.029
Sep 2007–Feb 2008							
Spotted owl	23	3 (1, 2)	1	0	2	0.896	0.044
Barred owl	22	1 (1, 0)	0	1	0	0.943	0.029
Mar–Aug 2008							
Spotted owl	25	3 (3, 0)	1	2	0	0.904	0.039
Barred owl	26	0	0	0	0	0.948	0.029
Sep 2008–Feb 2009							
Spotted owl	21	2 (0, 2)	2	0	0	0.897	0.043
Barred owl	26	2 (2, 0)	0	2	0	0.944	0.029
Cumulative (22 months)							
Spotted owl	29	9 (4, 5)	5	2	2	0.681	0.102
Barred owl	28	4 (3, 1)	0	4	0	0.815	0.075

^a Cause of death was determined by necropsy or evidence collected at recovery sites if remains were insufficient for necropsy analysis.

^b Weighted average of survival probabilities and unconditional standard errors (SE) estimated from all models with time effects.

Table 17. Ranking of top 10 known-fate models used to examine variation in survival (S) of radio-marked northern spotted owls and barred owls in western Oregon, USA, from 1 May 2007 to 28 February 2009. We show the intercept-only model without covariates, $S(.)$, and the fully parameterized model, $S(\text{Spp} \times t)$, for comparisons.

Model ^a	K	AIC_c	ΔAIC_c	AIC_c wt	Deviance
$S(\text{Spp} + \text{old} + \text{PHR})$	4	89.57	0.00	0.32	81.35
$S(\text{Spp} + \text{old})$	3	89.60	0.03	0.32	83.47
$S(\text{Spp} + \text{dedge} + \text{old})$	4	91.64	2.07	0.12	83.42
$S(\text{Spp} \times \text{old})$	4	91.68	2.11	0.11	83.47
$S(\text{Spp})$	2	95.77	6.20	0.01	91.71
$S(\text{Spp} + \text{old_core})$	3	95.93	6.36	0.01	89.80
$S(\text{Spp} + \text{PHR})$	3	96.00	6.43	0.01	89.87
$S(.)$	1	96.09	6.52	0.01	94.07
$S(\text{Spp} + \text{dedge})$	3	96.97	7.40	0.01	90.84
$S(\text{Spp} + \text{HR})$	3	97.02	7.45	0.01	90.89
$S(\text{Spp} + \text{edge} + \text{old_core})$	4	97.27	7.69	0.01	89.05
$S(\text{Spp} \times t)$	8	104.85	15.28	0.00	88.05

^a Key to model notation: K = number of covariates in the model; AIC_c = Akaike's Information Criterion corrected for small sample size; ΔAIC_c = difference between the AIC_c value of each model and the lowest AIC_c model; AIC_c wt = Akaike weight; Spp = species; old = mean proportion of old conifer forest in seasonal home ranges; old_core = proportion of old conifer forest in the breeding core-use area; dedge = mean distance to high-contrast edge; HR = proportion of the 95% fixed-kernel home range shared with heterospecific neighbors; PHR = probability of heterospecific presence within the 95% fixed-kernel home range. Time effects modeled as constant (.) or varying among 6-month time intervals (t).

seasons combined (2007–2009), spotted owls produced only 13 fledglings during 21 nesting attempts at 15 occupied territories. In contrast, barred owls produced 80 fledglings during 45 breeding attempts at 20 occupied territories. Barred owls also fledged more young per successful nest ($\bar{x} = 2.0$, range = 1–4 young) than spotted owls ($\bar{x} = 1.86$, range = 1–2 young). All 13 female barred owls that were radio-marked attempted to nest in all years they were monitored, and 12 of these females (92%) successfully fledged 49 young. Conversely, 10 (71%) of 14 female spotted owls that were radio-marked attempted to nest at least once during the study, but only 4 (29%) of these females successfully fledged 7 young.

In addition to differences in reproductive output, we also observed a marked difference between species in the estimated date of egg laying, with barred owls initiating nesting an average of 1 month earlier than spotted owls (Fig. 14). The estimated

mean date of clutch initiation was 9 March for barred owls (range = 2 Mar–24 Mar, $n = 17$) and 9 April for spotted owls (range = 30 Mar–29 Apr, $n = 10$). Based on a limited sample size, the number of young fledged per pair per year by spotted owls increased linearly with increasing distance from the nearest barred owl nest or territory center (slope coefficient $[\beta] = 0.387$, 95% CI = 0.124–0.649; $F_{1, 19} = 9.50$, $P = 0.006$). Five of 15 pairs of spotted owls attempted to nest within 1.5 km of a used barred owl nest, but all of these nesting attempts failed during incubation.

DISCUSSION

The recent colonization of the entire range of the northern spotted owl by barred owls provided a unique opportunity to investigate the emergence and possible consequences of interspecific competition between 2 previously allopatric and closely related avian predators. By directly monitoring spatial relationships, habitat use, diets, survival, and reproduction of sympatric spotted owls and barred owls, we identified a strong potential for interspecific competition and gained insight into the mechanisms and likely fitness consequences of competitive interactions between these species. We found a moderate to high level of overlap in use of space, habitat, and food resources between the 2 species. Spotted owls shared 10–56% of their seasonal and annual home ranges with individual barred owls in adjacent territories, and the 2 species displayed broadly similar patterns of habitat use within shared use areas. The species differed in that barred owls captured large numbers of small-sized terrestrial and aquatic prey that were rare or absent in diets of spotted owls. Despite this difference, however, we found that flying squirrels, woodrats, lagomorphs, tree voles, and deer mice were primary prey for both owl species in terms of dietary biomass, and overlap in diets increased during the nonbreeding season. The similarities we observed between spotted owls and barred owls in resource use indicated a high potential for exploitative competition, especially in times of low prey abundance or in cases where individuals shared overlapping foraging areas.

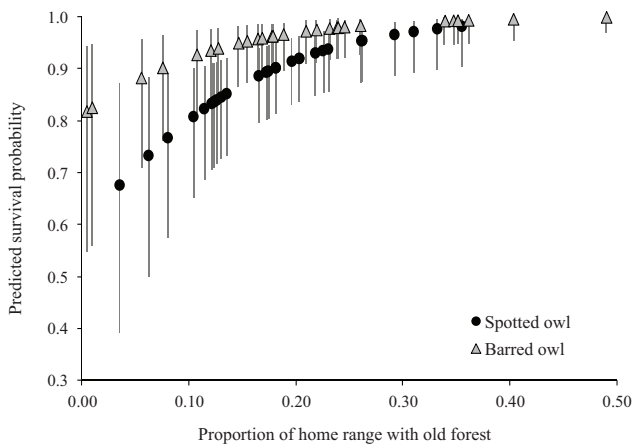


Figure 13. Predicted relationship between mean proportion of old conifer forest within the home range and seasonal (6-month) survival probabilities of radio-marked northern spotted owls ($n = 29$) and barred owls ($n = 28$) in western Oregon, USA, 2007–2009. We calculated point estimates with 95% confidence intervals at observed mean values for each individual under the best-supported model of survival, which included the additive effects of species and proportion of old conifer forest within the home range.

Table 18. Measures of nesting success and productivity of sympatric northern spotted owls and barred owls in western Oregon, USA, 2007–2009. Estimates are based on territorial pairs for which reproductive status was monitored from 1 March to 31 August of each year.

Year and species	Number of pairs	Number nesting (%) ^a	Number successful (%) ^b	Total young fledged	Young fledged per pair (SE)
2007					
Spotted owl	13	8 (62)	4 (50)	7	0.54 (0.24)
Barred owl	19	13 (68)	12 (92)	25	1.32 (0.27)
2008					
Spotted owl	14	10 (71)	1 (10)	2	0.14 (0.14)
Barred owl	20	15 (75)	14 (93)	26	1.30 (0.23)
2009					
Spotted owl	15	3 (20)	2 (67)	4	0.27 (0.18)
Barred owl	20	17 (85)	14 (82)	29	1.45 (0.27)
3-yr means					
Spotted owl	14	7 (50)	2.3 (33)	4.3	0.31 (0.11)
Barred owl	20	15 (75)	13.3 (89)	26.7	1.36 (0.14)

^a Percentage of pairs that attempted to nest.

^b Percentage of nesting pairs that successfully fledged ≥ 1 young.

In addition to overlaps in resource use, we also identified strong associations between the presence of barred owls and the behavior of spotted owls, as shown by changes in movements, habitat use, and reproductive output of spotted owls exposed to varied levels of spatial overlap with barred owls. Both species often used old conifer forest for foraging, and survival rates of both species were positively influenced by the amount of old forest available in their home ranges. This finding was particularly important, as it suggests that old forest was a potential limiting factor in the competitive relationship between the 2 species. This observation was also consistent with the results of Franklin et al. (2000), Olson et al. (2004), and Dugger et al. (2005), who independently found that the amount of old forest in territories of spotted owls had a positive influence on survival. The potential for barred owls to reduce fitness of neighboring spotted owls was further illustrated by our observation that nesting success of spotted owls declined with increasing proximity to a territory center of barred owls. When viewed collectively, our results suggest that a high density of barred owls can constrain the availability of critical resources for spotted owls through a combination of exploitation

competition for food and interference competition for territorial space.

Spatial Relationships

Understanding spatial relationships between interacting species requires primary information on the spatial ecology and individual life-history traits of each species. In particular, information on space use, site fidelity, and level of spatial overlap is required to assess potential segregation between species at the individual level, which in turn can determine species distributions at the population level. Spatial segregation is a particularly important determinant of resource partitioning in many birds of prey, where spacing among well-defined territories is often maintained by intra- and interspecific territoriality (Newton 1979, Solonen 1993, Katzner et al. 2003). Based on species-specific surveys of spotted owls and barred owls, there were >4.5 times as many territories occupied by barred owls than spotted owls in our study area. Territories with pairs of spotted owls were sparsely distributed with a mean nearest-neighbor distance nearly twice (4.5 km; 0.02 pairs per km²) that reported for the same region in the 1970s (2.6 km; Forsman et al. 1984). This change in the density of spotted owl pairs in our study area most likely reflected recent declines in spotted owl populations in the Oregon Coast Ranges (Anthony et al. 2006, Forsman et al. 2011). In contrast, the density of territories with pairs of barred owls was considerably greater, with a mean nearest-neighbor distance of 2.2 km (0.11 pairs per km²). The different spacing patterns among conspecific versus heterospecific owl pairs suggested that barred owls had a higher tolerance for spotted owls within their home ranges than for other barred owls. For example, nests used by barred owls in adjacent territories were always >1.9 km apart, whereas spotted owls sometimes nested (unsuccessfully) within 840 m of concurrently used barred owl nests. This pattern, which was also noted in western Washington (Hamer 1988), might be expected if intraspecific interactions had a stronger influence on spatial distribution of barred owls than interspecific interactions with spotted owls.

Spotted owls exhibit different patterns of space use in different portions of their geographic range, which is often attributed to regional differences in elevation, forest conditions, and availability of prey (Zabel et al. 1995, Noon and Franklin 2002). Mean

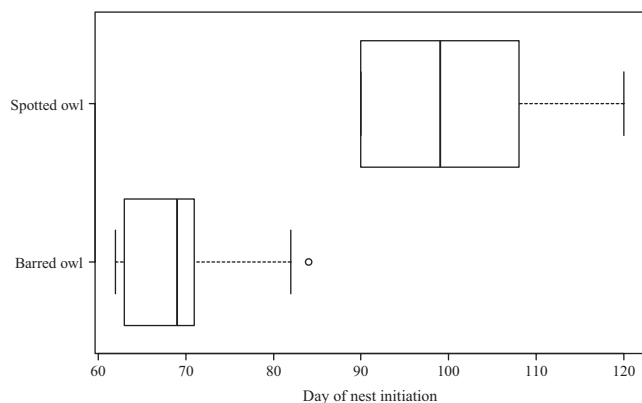


Figure 14. Ordinal date (day 1 = 1 Jan) of nest initiation for radio-marked female northern spotted owls ($n = 10$) and barred owls ($n = 17$) in western Oregon, USA, 2007–2009. The date of nest initiation was the first day we detected radio-marked females on a nest; median date of nest initiation was 9 March for barred owls and 8 April for spotted owls. Box plots bound the 25th and 75th percentiles, solid lines within boxes indicate the medians, and the whiskers extend to 1.5 times the interquartile range of the observations. Dots indicate extreme values.

(2,872 ha) and median (1,997 ha) estimates of annual home-range size (100% MCP) of individual spotted owls in our study were similar to those reported in the more fragmented landscapes of the central and southwest portions of the Oregon Coast Ranges by Forsman et al. (1984: $\bar{x}$ = 1,913 ha) and Carey et al. (1992: $\bar{x}$ = 2,908 ha). Our estimates tended to be larger, however, than for spotted owls in areas covered by more extensive and less fragmented old forests in western Oregon (Forsman et al. 1984: $\bar{x}$ = 1,177; Carey et al. 1990: $\bar{x}$ = 1,580 ha). Previous studies of spotted owls in western Oregon have reported that the size of home ranges may be influenced by the spatial distribution of old and mature forests, with larger home ranges found in more fragmented landscapes with limited availability of mature and old forest (Forsman et al. 1984, Carey et al. 1992, Carey and Peeler 1995, Glenn et al. 2004). Our results were consistent with these previous studies in that annual home-range size of spotted owls was negatively associated with cover of old forest in the home range, but this relationship was highly variable among individuals and relatively weak in our study. Instead, the most strongly supported predictor of annual home range size for spotted owls was the probability of barred owl presence in the breeding season home range, as determined by overlap of fixed-kernel UD's of radio-marked owls in adjacent territories. This result supported our prediction that spotted owls would respond to increased space sharing with barred owls by expanding their movements to include other areas. This response may have negative consequences for a central-place forager like the spotted owl, as the ability to increase the size of the home range and maintain territory ownership is likely limited by energetic and social constraints (Carey et al. 1992, Newton 1998, Ward et al. 1998).

Barred owls required less space for foraging and raising young than spotted owls despite their larger body mass and presumably greater energetic requirements. Estimates of mean (841 ha) and median (701 ha) annual home-range size (100% MCP) of barred owls in our study were similar to those reported for the north Cascades of Washington (Hamer et al. 2007; $\bar{x}$ = 781 ha, n = 22 owls, 95% adaptive fixed-kernel) and Saskatchewan (Mazur et al. 1998; $\bar{x}$ = 971 ha, n = 6, 100% MCP), but nearly twice as large as those reported in the eastern Cascades of Washington (Singleton et al. 2010; $\bar{x}$ = 416–477 ha, n = 9; 100% MCP). Comparisons of home-range size among these studies are confounded by differences in sample sizes and sampling intervals, but radio-telemetry studies that have been conducted on barred owls clearly show that they have smaller home ranges than spotted owls (Hamer et al. 2007, Singleton et al. 2010, also see reviews by Livezey 2007). Similar to spotted owls, we found a weak negative association between annual home range size of barred owls and the amount of old forest in the home range. None of the other environmental factors we examined, including the level of spatial overlap with spotted owls, explained a significant amount of variation in annual home range size of barred owls. The striking disparity in space use between the 2 species is perhaps best explained by differences in the scale of resource use by a generalist (barred owl) versus specialist (spotted owl) predator. Our dietary analysis illustrated that barred owls foraged opportunistically across a broad range of prey types and sizes, whereas spotted owls specialized on arboreal and semi-

arboreal mammals associated with older conifer forest. These observations support the hypothesis that barred owls have smaller home ranges relative to spotted owls because of interspecific differences in prey selection and foraging strategies (Hamer et al. 2001, 2007).

Both species used home ranges during the nonbreeding season that were approximately twice as large as those used during the breeding season. As in previous studies of spotted owls (Forsman et al. 1984, 2005; Carey et al. 1992; Glenn et al. 2004; Hamer et al. 2007) and barred owls (Elody and Sloan 1985, Hamer et al. 2007), patterns of home-range expansion during fall and winter reflected a variety of behaviors, including a general expansion in space use, a shift to a winter range that partially overlapped the breeding range, or a winter migration to an entirely separate area that was some distance from the breeding range. In our study, 21% of individual spotted owls exhibited winter migration behavior. Such movements were uncommon in barred owls, however, with most individuals remaining within 1–2 km of their nesting sites throughout the year. The species-specific differences in seasonal movements we observed may reflect differences in territorial behavior or dissimilar responses to seasonal changes in prey availability and weather. Regardless, the high density of barred owls in our study area, their strong year-round fidelity to nesting sites, and the low spatial overlap of seasonal home ranges among neighboring conspecifics were all indicators that barred owls maintained well-defined territories throughout the year. These observations are consistent with studies that monitored year-round movements of barred owls elsewhere (Nicholls and Fuller 1987, Hamer et al. 2007).

We used 3 complementary measures of home-range overlap to examine spatial interactions among radio-marked owls. These measures consistently indicated greater interspecific than intraspecific overlap among home ranges and core-use areas. Thus, if any form of interspecific territoriality was operating, it did not result in complete interspecific exclusion from home ranges. Our study confirmed that neighboring pairs of spotted and barred owls not only coexisted in close proximity, but also shared foraging areas within overlapping home ranges. In some cases, we observed both species occupying the same patch of old conifer forest within overlapping core-use areas (e.g., Fig. 6), but this type of spatial interaction was uncommon and largely restricted to cases in which newly colonizing barred owls were captured and radio-marked within the core-use area of spotted owls. Mean overlap between core-use areas of individual spotted and barred owls during the breeding season was relatively low (11%) compared to overlap among broader home ranges (38%). In cases where core-use areas did overlap, we found that the probability of locating a barred owl within a neighboring spotted owl's core-use area (0.09) was greater than the probability of locating a spotted owl within a barred owl's core-use area (0.03). Thus, aside from the few cases where we identified newly colonizing barred owls within a territory occupied by spotted owls, most individual spotted and barred owls did not share core-use areas during breeding or nonbreeding periods. Moreover, when space sharing did occur, it was almost always limited to the outer portion of the home range beyond an individual's core-use area (i.e., the most heavily defended portion of the home range). These results suggest some degree of interspecific territoriality

between the species, and that spatial segregation among core-use areas may have influenced their spatial distributions.

Habitat Use

Competition for space through territorial behavior is a clear example of interference competition. Nonetheless, to establish that differences in the spatial distributions of 2 species are due to interspecific territoriality, one must show not only that 1 species defends its territories against the other and the 2 do not have overlapping nesting territories, but also that the subordinate species would occupy habitats used by the dominant species if it were not prevented from doing so (Dhondt 2012). We investigated this concept in greater detail in our comparative assessment of habitat use, where we examined use of landscape features by spotted owls or barred owls relative to the known spatial distribution of each species in the study area. For spotted owls, we found that old conifer forest was the only forest type used for both foraging and roosting in proportions greater than its occurrence in the study area. This result closely parallels that of previous studies of habitat use and selection by spotted owls in the Douglas-fir-western hemlock zone of the central Oregon Coast Ranges (Forsman et al. 1984, Carey et al. 1992). Within their home ranges, foraging spotted owls most often used patches of old conifer forest that were within 2–3 km of nest sites, had steep (40–50°) slopes, and were within 300–400 m of a stream. We located spotted owls occasionally in young forests or along edges of recent clear-cuts, but use of these conditions was relatively uncommon. Rather, spotted owls spent a disproportionate amount of time foraging in steep ravines within patches of old conifer forest. Irwin et al. (2011) also observed use of steep slopes by spotted owls. Spotted owls in our study used riparian-hardwood forests along low-order streams more frequently than expected by chance. Solis and Gutiérrez (1990), Carey and Peeler (1995), Hamer et al. (2007), and Irwin et al. (2007, 2011) reported similar use of hardwood forests by northern spotted owls (but see Forsman et al. 2005). Our results also parallel those of Glenn et al. (2004), who reported that resource use by spotted owls in younger forests of western Oregon was associated with hardwood trees and riparian areas.

Habitat associations of barred owls have been described in a variety of different forest conditions throughout their geographic range. In eastern deciduous forests, they most often used mature and old mixed-forests in swamps and lowland riparian areas (Elody and Sloan 1985, Bosakowski et al. 1987). In boreal forests of Saskatchewan (Mazur et al. 1998) and in Alberta (Takats 1998, Olsen and Hannon 2006), barred owls used older mixed-conifer forests with trembling aspen (*Populus tremuloides*), but avoided young (<50 yr) forest and recent clear-cuts. Consistent with these descriptions, barred owls in our study used a broad mixture of forest types but were most strongly associated with gentle slopes in patches of structurally diverse, mature and old conifer forests or lowland riparian areas containing large hardwood trees. Use of older forest in combination with moist, valley-bottom forest was consistent with habitat associations described for barred owl nesting areas in Washington, USA (Herter and Hicks 2000, Pearson and Livezey 2003, Buchanan et al. 2004, Gremel 2005, Hamer et al. 2007). Although we found a high level of variation among

individuals in our study, foraging barred owls were equally likely to be found in riparian areas dominated by red alder and bigleaf maple trees or in patches of old conifer forest within 1 km of nests. Radio-marked barred owls in the eastern Cascades of Washington most often used areas that had larger tree-crown diameters, lower topographic positions, and gentler slopes (Singleton et al. 2010). Our finding that habitat use was most strongly associated with large conifer trees (>90 cm dbh) and hardwood trees on gentle slopes near streams were consistent with that pattern.

Spotted owls and barred owls in our study used foraging sites that were closer to streams than random locations, and the relative probability of use decreased linearly with increasing distance from a stream for both species. This result was in contrast to studies conducted in the Washington Cascades, which showed no strong association between resource use by barred owls and proximity to water (Hamer et al. 2007, Singleton et al. 2010). In our study area, small low-order streams were common in lower elevation riparian-hardwood zones and steep, narrow ravines in patches of mature and old conifer trees. Use of habitats near riparian zones has at least 3 explanations. First, cool microclimates associated with stream drainages may be favorable for thermoregulatory purposes during hot, dry summer months (Forsman 1976, Barrows 1981). Second, and perhaps more importantly, productive vegetation conditions near streams are likely to support a rich diversity of prey used by both owl species, including woodrats (Carey et al. 1999, Anthony et al. 2003), flying squirrels (Meyer et al. 2005, Wilson 2010), deer mice, and shrews (Verts and Carraway 1998). Stream habitats also provided a diversity of aquatic prey used by barred owls that were rare or absent from diets of spotted owls, such as salamanders, frogs, crayfish, snails, and fish. A third reason that riparian areas were used more frequently than other habitats may be because of their complex canopy structures that resulted from past fires that burned less intensively along stream corridors than in upslope areas (Reeves et al. 1989, Kauffman et al. 2001). Such structures may provide good perching opportunities for hunting terrestrial and arboreal prey. Differences between our study and those conducted in Washington, which showed no strong association between resource use by barred owls and proximity to water (Hamer et al. 2007, Singleton et al. 2010), could be caused by differences in how aquatic resources were quantified or by regional differences in how barred owls use streamside habitats. We note, however, that dietary analyses from these studies and ours were consistent in that barred owls tended to include amphibians and fish in their diets (Hamer et al. 2001, Graham 2012), which indicates some regional constancy in use of aquatic resources by barred owls.

High-contrast edges, mostly associated with clear-cuts, were another landscape feature that influenced use of foraging sites by both owl species. Although the effect was slightly stronger for barred owls, we found that the relative probability of use increased in a unimodal (convex) relationship with increasing distance to a forest-nonforest edge for both species. Thus, both species appeared to select foraging sites within the interior of forest patches, usually 300–500 m from edges. This finding is in slight contrast to other studies of resource use by spotted owls in the southern part of their geographic range, where owls foraged

disproportionately along or near edges of forest openings, perhaps in response to high densities of woodrats (Ward et al. 1998, Franklin et al. 2000). In northwestern Washington where woodrats are less abundant, Hamer et al. (2007) evaluated use of forest–nonforest edges by spotted owls and barred owls but found no clear relationship for either species. We had no data to suggest that woodrats were more or less abundant near forest edges, but in several cases, we did observe individual spotted and barred owls foraging along newly created forest–nonforest edges bordering active timber harvests. These observations were uncommon and may reflect a short-term response of owls taking advantage of vulnerable prey animals being displaced by ongoing timber harvest activities.

Resource-selection functions based on marked individuals have recently been used to show how the distribution of prey species can be shaped by predation risk from a dominant predator (Creel et al. 2005, Fortin et al. 2005, Hebblewhite et al. 2005), but few studies have used this approach to examine the functional relationship between the presence of a dominant competitor and patterns of habitat use by its subordinate. Results from our analysis provided clear evidence that descriptions of forest vegetation and physiographic conditions were not always sufficient in characterizing nighttime habitat use by spotted owls, as the presence of barred owls was also an influential factor. We found strong support for models of habitat use by spotted owls that accounted for the spatial distribution of core-use areas of barred owls, which supported our initial hypothesis that the presence of barred owls would alter resource selection by spotted owls. In contrast to spotted owls, we found no evidence that the spatial distribution of spotted owls influenced habitat use by barred owls. Spotted owls in our study responded to an increased likelihood of encountering core-use areas of barred owls by decreasing the time spent in mature and old forest and intensifying use of riparian-hardwood forests. A possible explanation for the increased use of riparian-hardwood forest by spotted owls in the vicinity of barred owls was that dietary segregation may be greatest in conditions that contain a wide diversity of terrestrial, moisture-dependent, and aquatic prey species for barred owls that are seldom used by spotted owls. Consequently, the potential for exploitation or interference competition might be reduced in riparian-hardwood forest types relative to older conifer forests.

Spatial avoidance of a dominant competitor by a subordinate is a common feature of species interactions (Palomares and Caro 1999, Dhondt 2012). The strong support for models including proximity to barred owls in our analysis of habitat use by spotted owls indicated that the influence of barred owls on resource selection extended beyond the core-use area and into the home range. Evidence that this response was associated with risk of predation by barred owls was equivocal, as we had no direct evidence that spotted owls were injured or killed by barred owls. Rather, we suggest that risk-sensitive resource use by spotted owls near core-use areas of barred owls represented an attempt to partition resources spatially, as would be expected if barred owls excluded spotted owls from their core-use areas via territorial aggression or mutual avoidance. Rather than avoiding areas used by barred owls altogether, spotted owls appeared to alter resource use to balance the probability of agonistic interactions with the

potential for energetic benefit, as suggested by an increased use of riparian habitats by spotted owls when in close proximity to barred owl core-use areas. This behavior was consistent with many other studies that show spatial segregation as a mechanism of niche partitioning among closely related bird species that occupy the same habitats (Cody 1974, Newton 1979, Jaksic 1985, Robinson and Terborgh 1995). Based on these observations, we suggest that the presence of barred owls rendered the preferred habitats of spotted owls less suitable in a manner similar to that of intraspecific territoriality among conspecific neighbors.

Diets and Foraging Behavior

As apex predators, spotted owls and barred owls are closely tied to the distribution and availability of their prey. Any explanation of differences in spatial distributions or habitat use between the species is, therefore, largely dependent on understanding the diets and foraging behavior of each species. Ecological separation of coexisting raptor species is often associated with differences in diet (Steenhof and Kochert 1988, Bosakowski and Smith 1992, Gutiérrez et al. 2007, Bilney et al. 2011), and diet appeared to be a contributor to niche differentiation between spotted owls and barred owls for a portion of the year in our study as well. The 2 species broadly overlapped in their use of mammalian prey, which represented the majority of dietary biomass, but we also identified differences in the sizes and activity behaviors of their most common prey. Spotted owls, for example, primarily captured arboreal and semi-arboreal prey such as flying squirrels, tree voles, and woodrats. Conversely, barred owls took more terrestrial and aquatic prey such as moles, shrews, salamanders, and crayfish. Barred owls were also more active in the daytime than spotted owls, as shown by the greater proportion of diurnal animals (e.g., Douglas squirrels, birds, reptiles) in diets of barred owls (18%) as compared to spotted owls (4%).

Differences we observed in diets of spotted owls and barred owls can only be partially explained by differential habitat use because the 2 species used similar forest types for foraging. Rather, segregation in diets must largely be explained by fundamental differences in foraging behavior between the 2 species, as shown by the high level of separation in the percent contributions of arboreal (52% vs. 26%), terrestrial (26% vs. 48%), and aquatic (0% vs. 4%) prey to dietary biomass of spotted owls and barred owls, respectively. This pattern of food-niche partitioning according to habitat strata was strikingly similar to that reported in a previous study of dietary overlap between spotted and barred owls in northwestern Washington (Hamer et al. 2001). Similar food-niche partitioning according to habitat strata has also been described for other specialist–generalist owl species that co-occupy the same habitats, including sooty owls (*Tyto tenebriosa*) and powerful owls (*Ninox strenua*) in southeastern Australia (Bilney et al. 2011), and the elegant scops-owl (*Otus elegans*) and Japanese scops-owl (*O. semitorques*) in Japan (Toyama and Saitoh 2011). Collectively, these studies and ours suggest that fine-scale partitioning of vertical space for foraging may be a mechanism contributing to ecological separation between closely related owl species. Thus, similar to MacArthur's (1958) well-known example of vertical niche differentiation among 5 closely related species of *Dendroica*

warbler, niche differences between spotted and barred owls also consisted of fine-scale differences in foraging techniques in the same habitats.

Diet composition of spotted owls in our study was similar to that reported for northern spotted owls throughout much of their geographic range, being dominated by flying squirrels, woodrats, tree voles, deer mice, and lagomorphs (Forsman 1976; Forsman et al. 1984, 2001, 2004; Ward 1990; Hamer et al. 2001). Diets of spotted owls in our study were also similar to those described in previous studies of spotted owls conducted in our study area during 1972–1980 (Forsman et al. 1984) and 1990–1995 (Thraillkill et al. 1998). These 2 studies and ours provide a unique historical timeline on diets of spotted owls before and after barred owls had reached high densities in the region. For example, the relative occurrence of flying squirrels in diets of spotted owls remained fairly constant across the 3 time frames that spanned a 37-year period (1972–1980: 35%; 1990–1995: 44%; 2007–2009: 38%; Forsman et al. 1984, Thraillkill et al. 1998, and our study, respectively). Proportions of other primary mammal species captured by spotted owls (e.g., woodrats, tree voles) were similar as well. This information suggests that barred owls may not necessarily be causing a shift in feeding ecology of spotted owls, but rather a reduction in prey availability or abundance.

Barred owls in our study captured a wide diversity of prey species at relatively low frequencies as has been reported elsewhere for this species (Elderkin 1987, Bosakowski and Smith 1992, Hamer et al. 2001). Despite the substantial use of insects, snails, shrews, and other small prey, however, the majority (89%) of biomass in the diets of barred owls was composed of mammals. Diets we observed in western Oregon slightly contrasted diets of barred owls in northwestern Washington, where the primary prey were snowshoe hares, flying squirrels, Douglas squirrels, and birds (Hamer et al. 2001). Also dissimilar to northwestern Washington, barred owls in our study captured large numbers of moles, shrews, small- to large-sized salamanders, crayfish, snails, and millipedes. Differences in diets of barred owls within the range of the northern spotted owl could be due to disparities in the distributions of preferred prey, latitudinal changes in prey species diversity, or temporal variation in prey use and availability among regions (Graham 2012).

Moderate dietary overlap among heterospecific neighbors (42%) and a relatively greater overlap in use of mammal prey (51%) suggested that the 2 species may compete for food, especially when prey are in short supply or in cases where both species shared the same foraging areas within overlapping home ranges. Flying squirrels, woodrats, and lagomorphs were primary prey for both owl species, as these species alone accounted for 81% and 49% of total dietary biomass for spotted owls and barred owls, respectively. Flying squirrels and hares were also primary prey for both spotted and barred owls in different areas of Washington (Hamer et al. 2001, Graham 2012). The degree of dietary overlap between spotted owls and barred owls in our study (42%) was less than in northwestern Washington during the 1980s (76%; Hamer et al. 2001). Differences in time frames, sample sizes, prey availability, and the manner in which prey species were categorized makes direct comparisons difficult, but these studies do indicate that the level of dietary overlap between

these species can vary regionally. In our case, regional differences in dietary overlap may have been partly due to differences in availability of shared prey, as woodrats have a restricted distribution and red tree voles do not occur in northwestern Washington (Verts and Carraway 1998).

Seasonal changes in prey availability may result in changes in potential for both interference and exploitation competition, particularly given our finding that spatial overlap varied little among seasons. A reduced level of interspecific territoriality during winter, for example, may decrease direct aggression near nest sites in a time when additional food constraints intensify exploitation competition for prey. We found that dietary overlap increased from 45% in the breeding season to 68% in the nonbreeding season. During the breeding season, many barred owls captured large numbers of prey species that are only seasonally available, including insects, amphibians, crayfish, or chipmunks. When these prey became less available during fall and winter, both spotted owls and barred owls converged on similar-sized prey such as flying squirrels and tree voles, and both owl species used larger areas, as shown by an increase in home range size. Our sample of prey was limited during the nonbreeding season, which makes conclusions regarding seasonal changes in diets less certain. Nonetheless, an increase in dietary overlap during the nonbreeding season was consistent with anticipated seasonal changes in availability of prey.

We identified differences in foraging strategies of spotted owls and barred owls, as shown by differences in timing and location of foraging activities as well as in the size of prey captured. Despite this evidence of dietary segregation, neighboring barred owls and spotted owls were similar in that 1) they captured predominantly nocturnal prey; 2) they spent much of their time foraging in old conifer forest and riparian areas; 3) they relied on many of the same mammal prey for the bulk of their dietary biomass (e.g., flying squirrels, woodrats, lagomorphs, red tree voles, and deer mice); and 4) their foraging areas often overlapped spatially. These similarities indicate a high potential for exploitative competition between the species. The specializations particular to each species and the seasonal differences we observed in dietary overlap further suggested that the intensity of exploitative competition may vary seasonally and spatially with changes in prey availability. The consequences of similar diets associated with older forests is that barred owls may reduce the density of spotted owl prey such that space-sharing spotted owls cannot find sufficient food for maintenance and reproduction, partially explaining the low productivity of spotted owls during our study.

Niche Relationships and Interspecific Territoriality

Species may reduce the potentially adverse effects of interspecific competition in a variety of different ways. For example, they may decrease spatial overlap in resource use with dominant competitors, change their diet, or change habitat use. Coexistence among other *Strix* owl species is typically sustained by separation of diets, space, foraging periods, foraging habitat, or a combination of these factors (see review by Gutiérrez et al. 2007). Measures of niche overlap in our study calculated for neighboring spotted owls and barred owls along space, habitat, and food resource dimensions showed that the 2 species were most similar in their use of available forest types (81%), followed by diets

(43%) and then spatial distributions (18%). Thus, niche separation between spotted owls and barred owls was largely driven by spatial segregation among home ranges and core-use areas. Data on habitat use and dietary composition suggested that riparian-hardwood forests may also affect resource partitioning between the species, but that use of older forest and the mammalian prey associated with these forest conditions was similar.

The measures of niche overlap we provided cannot be used to estimate the intensity of competition; however, they can be used to describe the potential for competition if resources that limit survival or reproduction are in short supply (Abrams 1980, Krebs 1998). Spotted owls and barred owls used patches of old conifer and riparian-hardwood forest in proportions 2–4 times their occurrence in the study area (<17% of total forested area; Appendix B), and the survival rates of both species were positively associated with the proportion of old forest within their home ranges. These lines of evidence suggest that old conifer forest represented a limiting resource for both owl species, especially when considered in the context of a high density of colonizing barred owls that have established their territories in remnant patches of old forest that are almost entirely restricted to public lands. Food is likely to be another limiting resource associated with older forest types, and the fact that spotted owls do not breed every year (Forsman et al. 2011) suggests that annual variation in prey abundance limits their reproduction as in other northern-latitude owl species (Korpimäki 1987, Hayward et al. 1993, Brommer et al. 2004) and many other birds (Newton 1998).

Aside from the subtle differences we observed in proportional use of old forest, slope conditions, and riparian areas, spotted owls and barred owls displayed broadly similar patterns of resource use. The species differentially used slope conditions within shared forest cover types across both spatial scales of analysis, which was a result similar to previous studies showing that barred owl nests were located on gentler slopes than those used by spotted owls (Herter and Hicks 2000, Pearson and Livezey 2003, Buchanan et al. 2004, Gremel 2005). Moreover, by linking data on habitat use with concurrent information on owl diets, it was clear that the 2 species focused on different habitat strata, with barred owls preying more heavily on terrestrial species and spotted owls preying more heavily on arboreal mammals. This finding suggested that segregation in habitat use may have been operating along vertical space (e.g., canopy or understory height), a dimension of resource partitioning that we did not examine. This form of trophic partitioning may not have been particularly effective in our study area, however, particularly given the high density of barred owls and sparse availability of the most commonly used forest types. Future studies could provide a better understanding of the relative importance of vertical forest structure to spotted owls and barred owls by using remote sensing technologies that characterize above-ground forest structure (e.g., light detection and ranging [LiDAR]).

Our measures of ecological overlap generally fell below 0.50. The few cases where ecological overlap was >0.50 represented situations in which a high amount of spatial overlap occurred between the core-use areas of newly colonizing barred owls and resident pairs of spotted owls. For the most part, however, individual spotted and barred owls did not share core-use areas.

This pattern of spatial segregation provided key insight on the niche relationships between these species. When resources are limiting, for example, many bird species will defend their breeding territories not only against conspecifics but also against individuals of different species (Newton 1979, Jaksic 1985, Van Lanen et al. 2011). The broad similarity in patterns of habitat use suggested that spatial segregation among core-use areas was most likely a result of territorial interactions (interference competition) rather than differences in the way individuals used available forest conditions. Spatial avoidance of barred owl nesting areas by spotted owls in our study most likely reflected a combination of indirect (e.g., territorial calling) and direct (e.g., being chased) interactions. The potential for barred owls to physically exclude spotted owls from their territories was shown by Van Lanen et al. (2011), who used a call playback experiment to quantify aggressive behavior of spotted and barred owls during territorial interactions. Barred owls in their study responded with higher levels of vocal and physical aggression than did spotted owls when artificial agonistic confrontations occurred, suggesting that barred owls assumed the dominant role during territorial interactions. Van Lanen et al. (2011) concluded that interference competition was likely occurring, and that spotted owls may attempt to reduce the frequency of agonistic interactions with barred owls through spatial avoidance. This behavior appeared to be the case in our study where the smaller subordinate species (spotted owls) appeared to reduce the potential for agonistic interactions through spatial avoidance of core-use areas of barred owls. An increasing number of barred owls that locate and defend their territories within habitats historically occupied by spotted owls could be a major obstacle for colonizing spotted owls, as has been indicated by several long-term studies of occupancy dynamics in spotted owls (Olson et al. 2005, Kroll et al. 2010, Dugger et al. 2011).

Survival and Reproduction

Barred owls in our study area displayed demographic superiority over spotted owls; known-fate estimates of annual survival was greater for barred owls (0.92) than for spotted owls (0.81), and mean reproductive output of pairs of barred owls was 4.4 times greater than that of spotted owls over a 3-year period. Estimates of annual survival for spotted owls in our study were slightly less than concurrent estimates of apparent survival of adult (≥ 3 yr) spotted owls in 2 adjacent demographic study areas in western Oregon (Oregon Coast Ranges: $\phi = 0.86$, Tyee: $\phi = 0.86$; Forsman et al. 2011:32). Known-fate and apparent survival estimates from capture-recapture studies are typically not comparable (i.e., $\phi = \hat{S}$ only when permanent emigration is 0), but this comparison was useful in our case because 1) permanent emigration of adult spotted owls observed in long-term demographic studies of color-marked individuals is minimal (2–3% per year; Forsman et al. 2011); and 2) our estimates of survival were free of bias associated with unknown mortality or emigration of radio-marked owls. We found no published estimates of survival for barred owls, but annual survival of barred owls in our study (0.92) was greater than estimates reported for adult spotted owls (range = 0.82–0.87; Forsman et al. 2011:32).

Our analyses suggested that increasing proportions of old forest within seasonal home ranges had a positive influence on adult

survival probability of both spotted owls and barred owls. The relationship we examined between survival and the probability of heterospecific presence in the home range was negative as predicted, but this effect was relatively weak. Rather, models that received the greatest support from our data showed that survival of both species declined linearly with the percentage of old forest in seasonal home ranges. This finding is similar to the results of Franklin et al. (2000), Olson et al. (2004), and Dugger et al. (2005), who found that apparent survival of spotted owls was positively associated with cover of older forest within concentric circles surrounding nest trees or territory centers. The primary mechanisms through which this relationship is likely to arise is that the structural diversity of old forests may provide 1) more optimal structure for pursuing and capturing prey; 2) greater densities of mammalian prey such as flying squirrels (Carey et al. 1992, Holloway and Smith 2011) and red tree voles (Dunk and Hawley 2009); and 3) refuges and escape routes from large avian predators (Forsman et al. 1984, Franklin et al. 2000, Hakkarainen et al. 2008).

Despite the uncertainty associated with predation events of spotted owls, we had no evidence that spotted owls were wounded or killed by barred owls. We did, however, find direct evidence that great horned owls predated at least 2 spotted owls in our study. Great horned owls have been identified as a primary cause of death for spotted owls in previous studies in western Oregon as well (Forsman et al. 1984, Carey et al. 1990). Although great horned owls are also a common predator of barred owls (Mazur and James 2000), predation was not identified as a cause of death for barred owls in our study. Great horned owls were regularly observed within more open habitats or near forest edges in our study area during nighttime surveys and radio-telemetry monitoring activities, and these large predators may prefer highly fragmented landscapes for foraging (Johnson 1993, Rohner and Krebs 1996). In our study area, forest fragmentation was primarily a result of clear-cutting, which could increase predation rates on spotted owls by favoring predators that use edges or more open landscapes, such as great horned owls and red-tailed hawks (*Buteo jamaicensis*). Despite this potential, we found no evidence that the amount of time that radio-marked owls spent near forest edges was associated with survival for either species, perhaps because of the course nature of this covariate in our analysis.

We found that pairs of barred owls produced an average of 4.4 times as many young as pairs of spotted owls. The mean percentage of spotted owl pairs that attempted to nest during 2007–2009 (50%, $n = 42$ nesting opportunities) was similar to previous estimates obtained in our study area during 1990–1995 (44%, $n = 117$ nesting opportunities; Thraill et al. 1998:17). In our more recent study, however, the mean percentage of nesting pairs of spotted owls that successfully fledged young (33%) was substantially less than historical estimates (64%; Thraill et al. 1998:17), which may reflect a greater rate of nesting failure in 2007–2009. Our estimates of the mean number of young fledged per pair of spotted owls ranged from 0.14 in 2008 to 0.54 in 2007, which was at the lower end of historical values reported in our study area before barred owls had reached high numbers (range = 0.09–1.35; Thraill et al. 1998:18). In the first 2 years of our study, the proportion of spotted owl and barred

owl pairs that attempted to nest was similar. Thus, the marked difference in reproductive output between species in these years was largely due to a greater rate of nesting failure of spotted owls, as 32–90% of pairs that attempted to nest failed to produce young. In the third year of our study, the percentage of spotted owls that attempted to nest dropped to 20%, whereas the proportion of barred owls that nested increased to 85%.

The specific cause of nesting failures for spotted owls in our study was unknown, with few exceptions. In 1 case, a radio-marked male spotted owl with nestlings was predated by a great horned owl, at which point the adult female spotted owl (also radio-marked) abandoned the nest, moved to a different territory, and paired with a different male. In 2 other cases of nesting failure by spotted owls, we documented barred owls from adjacent territories (usually males) vocalizing in close proximity (<100 m) to nest trees where female spotted owls were incubating eggs. In these situations, we often observed female spotted owls flushing from their nests and initiating a series of aggressive vocalizations, apparently in response to the nest site intrusion by a vocalizing barred owl. Whether barred owls were the cause of these nest failures was difficult to determine. However, because of the mismatch in the timing of egg-laying between the species, nesting pairs of spotted owls commonly were still in the early stages of incubation when their nearby barred owl neighbors already had nestlings with increasing food requirements.

The 1-month difference we observed in nest-initiation dates between spotted owls and barred owls may have important consequences on site occupancy, nesting success, and niche relationships of these species. One potential competitive advantage of early nesting by barred owls is the avoidance of competition with spotted owls for nest sites, as many spotted owls did not return to their breeding areas until late February when barred owls had already selected a nest site and initiated incubation. Hence, the mismatch in breeding phenologies may allow barred owls to usurp nesting areas of spotted owls still engaged in winter migration activities. Another predicted consequence of interspecific competition is a shift in the niche of 1 or more of the competing species (Diamond 1978, Grant 1986). For example, competition for a similar set of resources (i.e., nest cavities and food) over time could lead to delayed nesting in spotted owls to reduce overlap in breeding phenologies with barred owls, as has been demonstrated in studies of competitive interactions between Tengmalm's owls (*Aegolius funereus*) and Ural owls (*Strix uralensis*; Hakkarainen and Korpimäki 1996) and cavity-nesting birds and invasive European starlings (*Sturnus vulgaris*; Ingold 1996, Wiebe 2003). Spotted owls may also be less vocal in the presence of barred owls (Crozier et al. 2006), which could lead to delays in pair formation during courtship. In addition, males engaged in territorial encounters with neighboring barred owls may not be able to invest much time in courtship feeding, which could delay the start of egg-laying because females rely almost entirely on food provided by males during egg production.

Experimental evidence has shown that interspecific interactions among raptors can negatively influence species-specific reproduction. Krüger (2002), for example, showed that an experimentally increased artificial goshawk (*Accipiter gentilis*) threat near the

nests of common buzzards (*Buteo buteo*) substantially decreased reproductive output. Buzzards who failed to produce young under artificial predation risk also abandoned their territories frequently (Krüger 2002). In our study, inferences concerning the effects of barred owls on reproduction of spatially associated spotted owls were somewhat restricted by small sample sizes and a limited study period (3 yr). Moreover, we did not evaluate other factors that can influence reproductive output of spotted owls such as forest structure and weather (Franklin et al. 2000, Olson et al. 2004, Glenn et al. 2011b). Despite these potential limitations, our analyses provided evidence that the number of young fledged by spotted owls decreased with increasing proximity to barred owl nests or territory centers. In addition, all spotted owls that attempted to nest within 1.5 km of a territory center occupied by barred owls failed to successfully produce young. Intraguild predation did not explain this pattern because we found no evidence of predation of adult or nestling spotted owls by barred owls. Rather, joint use of common resources leading to food depletion in combination with agonistic interactions with neighboring barred owls during critical stages of nesting may have jointly affected breeding performance of spotted owls, as has been shown in long-eared owls (*Asio otus*; Nilsson 1984) and some diurnal raptors (Krüger 2002, Carrete et al. 2006). This finding has broad implications for the future conservation of spotted owls, as it suggests that spatial heterogeneity in fitness potential may not arise solely because of differences among territories in the quality of forest conditions or landscape configurations (e.g., Franklin et al. 2000, Olson et al. 2004, Dugger et al. 2005), but also because of the spatial distribution of a newly established competitor.

Conclusions

Our observations on the ecological relationship between spotted owls and barred owls satisfy several of the most stringent criteria proposed for establishing the existence of interspecific competition in birds, including: 1) resource use between potential competitors must overlap; 2) resource use of 1 species affects the resource use (availability) of the other; and 3) the fitness potential of individuals is reduced by the presence of individuals of another species (MacNally 1983, Wiens 1989, Newton 1998, Dhondt 2012). Both species commonly used patches of older conifer forest for roosting and foraging, they both relied on similar prey associated with these forest types, and survival of both species was positively influenced by increasing amounts of old conifer forest in their home ranges. These findings highlighted the influence of old forest as a potential limiting factor in the competitive relationship between the 2 species. Our analyses of species-specific variation in home-range size and nighttime resource selection further indicated that barred owls altered space use and foraging behavior of spotted owls, which may have both direct and indirect consequences to fitness of spotted owls. In addition to behavioral consequences, we also identified a high potential for exploitation competition among spatially associated spotted owls and barred owls, as shown by their broadly overlapping spatial distributions, similarities in habitat use, and shared use of mammalian prey such as flying squirrels and tree voles. These findings are consistent with previous reports of reductions in site occupancy, survival, and fecundity of spotted owls when barred

owls were detected in their territories (Kelly et al. 2003; Olson et al. 2004, 2005; Anthony et al. 2006; Kroll et al. 2010; Dugger et al. 2011; Forsman et al. 2011; Glenn et al. 2011a, b). Taken together, these studies and ours support the hypothesis that a combination of exploitation and interference competition with increasing populations of barred owls are interacting with other limiting factors to negatively influence vital rates of spotted owls.

Despite the moderate to high level of ecological overlap we observed, spotted owls and barred owls displayed subtle differences in space use, habitat use, foraging behavior, and diets. Differential patterns of resource use by spotted and barred owls in our study likely reflected trade-offs between individual goals, such as the need to occupy certain forest types yet avoid obstacles like competitors and predators. Spotted owls may attempt to reduce competitive interactions with barred owls by spatial avoidance. However, in doing so, they may limit the amount of resources available to them and experience increases in predation risk, as suggested by the high incidence of avian predation on spotted owls in our study. Ultimately, spatial segregation among core-use areas and subtle differences in foraging strategies between spotted owls and barred owls may only be effective mechanisms of resource partitioning in situations where resources are not strongly limiting, or when densities of barred owls are low. With interspecific territoriality acting in conjunction with exploitative competition for a common set of limited resources, however, high densities of barred owls are likely to have a significant impact on spotted owl populations that are already in flux because of climatic variation or loss of habitat. We therefore conclude that an increasing population of barred owls could affect viability of spotted owls both directly (via spatial exclusion from critical resources) and indirectly (via joint exploitation of mammalian prey in common foraging areas).

Our study cannot be used by itself to directly assess whether barred owls are responsible for continuing declines in spotted owl populations. Such a determination would have required experimental removal of barred owls from the study area to observe the demographic response of spotted owls (Buchanan et al. 2007, Gutiérrez et al. 2007). Moreover, the ecological relationships we observed between spotted owls and barred owls within the fragmented matrix of federal and industrial forests of western Oregon may not be representative of relationships between these species in more contiguous or drier forests, higher elevations, or in areas where owl densities or prey availability are different. In particular, resource availability in our study area likely was limited by the unique distribution of land ownership, which resulted in a fragmented patchwork of mature and old forests that occurred almost entirely on public lands. Consequently, researchers and managers should be cautious about extrapolating our results beyond the central Oregon Coast Ranges.

Our study was observational in that it lacked an experimental control, but by directly monitoring resource use and demographic traits, we provided strong evidence for interspecific competition between spotted owls and barred owls. Moreover, we note that our study serves as an updated replicate to a similar study on resource use by spotted owl and barred owls conducted in northwestern Washington in the 1980s (Hamer et al. 2001,

2007). Many of the results between these 2 studies were similar, which further strengthens the interpretation of our results and our scope of inference. A particularly important finding in our study was that old forests represented high-quality habitat for both owl species in terms of its influence on adult survival, which is the demographic trait that most strongly influences population growth rates of spotted owls (Noon and Biles 1990) and many other long-lived birds (Sæther and Bakke 2000). This finding, along with evidence that the presence of barred owls reduced the amount of old forest available to spotted owls, suggests that spatially structured social aspects such as the presence and distribution of a newly established competitor constitutes an emergent and critically relevant threat to spotted owls.

MANAGEMENT IMPLICATIONS

The addition of new species to landscapes is as important to consider in managing wildlife populations as is species loss. Biological invasions are second only to direct habitat loss as a threat to imperiled species in the United States (Wilcove et al. 1998), and the combined constraints these stressors can place on native wildlife populations has been exemplified by challenges associated with the conservation and management of northern spotted owls (Noon and Franklin 2002, Buchanan et al. 2007, Gutiérrez et al. 2007, USFWS 2011). The causes of the barred owl range expansion into western North America are ultimately unknown, but some authors have suggested that landscape changes caused by humans (Livezey 2009) or gradual changes in climate (Monahan and Hijmans 2007) enabled barred owl populations to expand beyond their historical geographic range in eastern North America. Regardless, the emergent threat of barred owls to spotted owls emphasizes the importance of considering native invaders in a management context, particularly as species' distributions become modified by habitat loss or gain caused by changes in climate and land use (Walther et al. 2002, Carey et al. 2012). Results from our study indicate a strong potential for both exploitation and interference competition between spotted owls and recently established barred owls, and that availability of old forests and associated prey species are likely to be the most strongly limiting factors in the competitive relationship between these species. Our findings have 3 major implications for land managers to consider in conservation strategies for spotted owls and their habitats: 1) the importance of maintaining high-quality habitat in late-successional forests; 2) options to mitigate the apparent impacts of increasing populations of barred owls; and 3) the potentially cascading effects of barred owls on other native wildlife in the Pacific Northwest.

The management and conservation of remaining old forests, which is a chief focus of recovery strategies for northern spotted owls (Forest Ecosystem Management Assessment Team 1993, USFWS 2011), is a major source of socio-economic controversy in the Pacific Northwest. Our results emphasize the value of old conifer forests, large hardwood trees, and moist bottomland riparian areas to both spotted owls and barred owls in the central Oregon Coast Ranges. These findings support the conclusions of Dugger et al. (2011) and Forsman et al. (2011) in that the existence of a new and potential competitor like the barred owl

makes the protection of old forest habitat even more important because any loss of habitat will likely further constrain the 2 species to the same set of limited resources, thereby increasing competitive pressure and leading to additional negative impacts on spotted owls. Our additional observation that riparian-hardwood forests along low-order streams may facilitate niche segregation between the 2 species highlights the importance of considering these unique forest conditions within a management context. Riparian forests support a wide diversity of aquatic and terrestrial prey used by both spotted and barred owls, but are shorter-lived than conifer forests because of natural differences in succession. Moreover, riparian forests on small headwater streams in the Oregon Coast Ranges generally receive less protection from anthropogenic disturbance than larger fish-bearing streams, in part because of a focus on the role of riparian vegetation in fish conservation (Oregon Department of Forestry 2010).

A question common to invasive species, native or non-native, is whether control programs effectively mitigate impacts (Shine and Doody 2011). Underlying this question is how society values the species involved, which may or may not align with the ecological- or policy-related goals of maintaining natives and eliminating invaders. There are clear limitations to the actions that can be taken to control barred owls and their negative impact on spotted owls (Buchanan et al. 2007). Although it is currently unknown if control of barred owl populations is a feasible means of conserving spotted owl populations, our analyses and others (e.g., Dugger et al. 2011, Forsman et al. 2011) clearly show that further loss of contiguous older forests with an increasing population of barred owls can act synergistically to increase competitive pressure on spotted owls and negatively affect their vital rates. Therefore, we predict that competitive release from barred owls will result in decreases in space use and energy expenditure with corresponding increases in site occupancy and reproductive output of spotted owls, but only if sufficient nesting, roosting, and foraging habitats are available for re-occupancy by spotted owls and their prey. We further posit that competitive release from barred owls would be most apparent in areas with contiguous older conifer forests, as these conditions appeared to be a primary source of resource limitation and overlap between the species in our study in western Oregon and in the studies of Hamer et al. (2001, 2007) in northwestern Washington.

Conversely, our finding that niche overlap between spotted owls and barred owls may be lowest in moist riparian-hardwood habitats, and that barred owls may be more tolerant of spotted owls in these conditions, indicates that control of barred owls in these areas may have a less noticeable influence on population characteristics of spotted owls than in older conifer forests. Experimental removal of barred owls could be used to test our predictions and determine whether localized control of barred owl occurrence is an ecologically practical and socio-politically suitable management tool to consider in future conservation strategies for spotted owls. Experimental removal of barred owls could also provide an answer to whether sufficient numbers of nonbreeding spotted owls are available in landscapes to recolonize historical nesting territories. We emphasize that the decision of whether or not to implement localized control of barred owl numbers as a management tool to conserve spotted

owls is a social one that can be guided but not defined by scientific input.

Rapid increases in populations of a predatory invader like the barred owl can pose a variety of threats to native fauna and flora because even small shifts in relative abundance among species in a community can lead to substantial changes in food-web dynamics (Schmitz et al. 2000, Valéry et al. 2009). For example, Schmidt (2006) showed that an artificially increased threat of barred owl predation (playback of owl vocalizations) altered the space-use patterns of white-footed mice (*Peromyscus leucopus*), which in turn had a significant indirect effect on predation rates of songbird nests. In a similar experiment, Schmidt and Belinsky (2013) demonstrated that an artificial predation risk in the form of simulated barred owl vocalizations reduced the dusk singing behavior of a diurnal passerine, the veery (*Catharus fuscescens*). Vole species exposed to artificially manipulated cues of owl presence also have shown physiological and behavioral changes consistent with anti-predator behavior, including reductions in overall activity and use of different microhabitats (Hendrie et al. 1998, Eilam et al. 1999). Total impact of a newly established predator on a native community might be a function of both increased predator abundance and prey susceptibility as habitats are modified (Didham et al. 2007). Given the high density and reproductive output of barred owls in the heavily managed forests of our study area, we believe that their effects on prey behavior and abundance are likely to have already materialized. Land managers and researchers should be aware of the potentially strong cascading effects that barred owls may have on the native wildlife community beyond spotted owls, and our study provided a baseline sample of species that may be susceptible to these effects.

SUMMARY

- Repeated surveys of spotted owls and barred owls in a 975-km² forested study area in western Oregon, USA, showed that the number of territories occupied by pairs of barred owls (82) greatly outnumbered those occupied by pairs of spotted owls (15).
- Home ranges of spotted owls estimated for breeding, nonbreeding, and annual time periods averaged 2–4 times larger than those estimated for barred owls.
- Interspecific overlap of home ranges was greater than intraspecific home-range overlap among owls radio-marked in adjacent territories. We observed a moderate to high level of interspecific space-use sharing within home ranges of neighboring pairs of spotted and barred owls, but minimal spatial overlap among core-use areas.
- The probability of locating a barred owl in the home range of a neighboring spotted owl was greater than the probability of locating a spotted owl within the home range of a neighboring barred owl. This directional pattern of spatial overlap was consistent among sexes, seasons, and years. Spatial segregation between the 2 species' core-use areas was suggestive of interspecific territoriality, a clear indication of interference competition.
- We found a strong, positive association between annual home-range size of spotted owls and the extent of barred owl presence

within the home range, suggesting that spotted owls responded to an increased level of space-use sharing with neighboring barred owls by expanding their movements to include other areas.

- Both species used patches of old (>120 yr) conifer forest in proportions 2–5 times greater than expected based on occurrence, and both species used riparian-hardwood forest along streams for foraging. Barred owls used available forest types more evenly than spotted owls, but were most strongly associated with patches of large hardwood and conifer trees that occupied relatively flat areas. Conversely, spotted owls spent a disproportionate amount of time foraging and roosting in forests with large (>50 cm dbh) conifer trees along steep slopes in ravines. We found no evidence that the 2 species differed in their use of open areas or young, mature, or riparian-hardwood forest types. Mean overlap among individual spotted and barred owls in proportional use of primary forest types was 81% (range = 30–99%).
- The presence of barred owls altered patterns of habitat use by spotted owls, as shown by a decline in the relative probability of use by spotted owls as proximity to the core-use area of a barred owl increased. This result was consistent with patterns of spatial segregation between the species, which provided further evidence of interference competition.
- Barred owls foraged opportunistically across a broad range of prey sizes and types, whereas spotted owls specialized on arboreal mammals associated with mature and old forests. Flying squirrels, woodrats, and lagomorphs were among the primary prey items for both owl species in terms of dietary biomass. Mean interspecific dietary overlap among neighboring pairs of spotted and barred owls was moderate (42%; range = 28–70%).
- Barred owls exhibited demographic superiority over spotted owls; the estimated annual survival probability was greater for barred owls (0.92, SE = 0.04) than for spotted owls (0.81, SE = 0.05), and mean reproductive output of pairs of barred owls was 4.4 times greater than that of spotted owls over a 3-year period.
- The percent cover of old forest habitat within home ranges was positively associated with seasonal (6-month) survival probabilities of both owl species. We found no evidence that spotted owls were killed or predated by barred owls, and survival probabilities of spotted owls were not strongly influenced by the amount of spatial overlap with barred owls in adjacent territories.
- The number of young fledged per pair per year by spotted owls decreased linearly with decreasing nearest-neighbor distances between the nest sites of the 2 species. No spotted owls that attempted to nest within 1.5 km of a concurrently used barred owl nest successfully produced young during the study.
- Our study provided strong support for predictions concerning a negative effect of barred owls on movements, resource selection, and reproduction of spotted owls. Our study cannot be used by itself to directly assess whether barred owls are responsible for ongoing declines in spotted owl populations, but our results can be considered in concert with well-designed experiments to help inform decisions regarding the future management of spotted owls and their habitats.

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APPENDIX A. ACCURACY ASSESMENT OF FOREST VEGETATION MAP.

We determined accuracy of the classified forest map based on ground sampling completed at 141 random test plots within the study area. Forest vegetation measurements at reference plots were obtained from 2 sources: 1) visits to randomly selected grid coordinates to measure size (dbh), species composition, and approximate age of dominant and co-dominant trees ($n = 47$); and 2) forest vegetation inventory plot measurements obtained from private timber companies ($n = 94$). We estimated accuracy of forest cover types by comparing predicted and observed conditions measured at landscape locations using a standard matrix of classification error (Congleton and Green 2008).

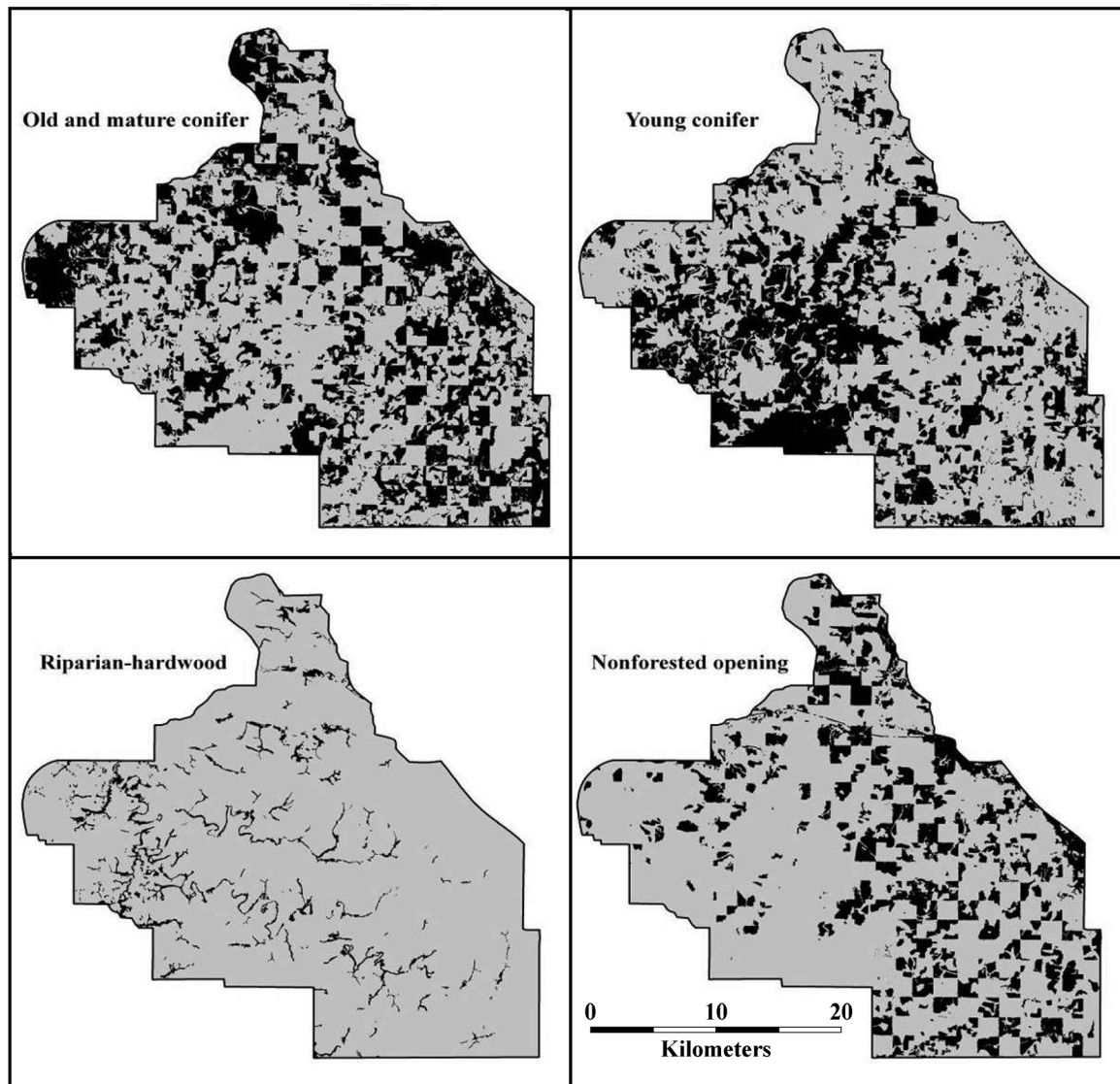
Predicted forest type ^a	Observed forest type					Total	User's (%) ^b
	Young conifer	Mature conifer	Old conifer	Riparian-hardwood	Nonforest		
Young conifer	55	2		1		58	94.8
Mature conifer	9	12	3			24	50.0
Old conifer		2	16			18	88.9
Riparian	1			6	1	8	75.0
Nonforest	4	1		1	27	33	81.8
Total	69	17	19	8	28	141	
Producer's (%) ^b	79.7	70.6	84.2	75.0	96.4		Overall accuracy 82.3%

^a Reference plots that were mapped correctly fall along the diagonal in gray.

^b Producer's accuracy measures the error of exclusion, user's accuracy measures the error of inclusion.

APPENDIX B. DISTRIBUTION OF PRIMARY FOREST TYPES ON THE WESTERN OREGON STUDY AREA, USA, 2009.

Forest types and their proportional representation on the study area were: old conifer (16,873 ha, 17%), mature conifer (20,953 ha, 21.1%), young conifer (33,796 ha, 34%), riparian-hardwood (4,800 ha, 4.8%), and nonforest (20,673 ha, 20.8%). Nonforest was primarily recent clear-cuts on private and state lands.



APPENDIX C. A PRIORI MODELS USED TO CHARACTERIZE NIGHTTIME HABITAT USE BY NORTHERN SPOTTED OWLS AND BARRED OWLS IN WESTERN OREGON, USA, 2007–2009.

Hypothesized effects	Model ^a
Influence of forest type and central place foraging	
Null model (resource selection is random)	No effects model
Resource selection is dependent on forest type only	Fortype
Additive effect of forest type and distance to nest	Fortype + dnest
Effect of forest type and distance to nest (poly)	Fortype + dnest + dnest ²
Influence of patch-scale forest structural conditions	
Effect of density of large (>50 cm dbh) conifers	TPHcon50
Effect of quadratic mean diameter of conifers	QMDcon
Nonlinear effect of quadratic mean diameter of conifers	QMDcon + QMDcon ²
Effect of basal area of hardwoods	BAhdw
Nonlinear effect of basal area of hardwoods	BAhdw + BAhdw ²
Effect of canopy cover of hardwoods	CANCOVhdw
Nonlinear effect of canopy cover of hardwoods	CANCOVhdw + CANCOVhdw ²
Nonlinear effect of quadratic mean diameter of conifers and canopy cover of hardwoods	QMDcon + QMDcon ² + CANCOVhdw + CANCOVhdw ²
Nonlinear effect of quadratic mean diameter of conifers with linear effect of canopy cover of hardwoods	QMDcon + QMDcon ² + CANCOVhdw
Best forest structure model with additive effect of distance to nest (poly)	(best from 5 to 13) + dnest ²
Influence of slope, edge, and moisture	
Best structure from 1 to 14 above with effect of slope	(best from 1 to 14) + slope
Best structure from 1 to 14 above with additive effect of distance to high contrast edge	(best from 1 to 14) + dedge
Best structure from 1 to 14 above with quadratic effect of distance to high contrast edge	(best from 1 to 14) + dedge + dedge ²
Best structure from 1 to 14 above with additive effect of distance to stream	(best from 1 to 14) + dstream
Best structure from 1 to 14 above with quadratic effect of distance to edge and distance to stream	(best from 1 to 14) + dedge + dedge ² + dstream
Best structure from 1 to 14 above with additive effect of slope and distance to stream	(best from 1 to 14) + slope + dstream
Best structure from 1 to 14 above with additive effect of slope and quadratic distance to edge	(best from 1 to 14) + slope + dedge ²
Best structure from 1 to 14 above with additive effect of slope, quadratic distance to edge, and distance to stream	(best from 1 to 14) + slope + dedge ² + dstream
Influence of heterospecific neighbors	
Best structure from 1 to 22 above with additive effect of proximity to heterospecific core-use area	(best from 1 to 22) + dHET
Best structure from 1 to 22 above with additive effect of area within heterospecific core-use area	(best from 1 to 22) + HETcore
Best structure from 1 to 22 above with an interaction between proximity to heterospecific core use area and old conifer forest type	(best from 1 to 22) + dHET + (OLD × dHET)
Best structure from 1 to 22 above with an interaction between proximity to heterospecific core use area and riparian-hardwood forest type	(best from 1 to 22) + dHET + (HDW × dHET)

^a See Table 1 for a description of covariates included in models.

APPENDIX D. A PRIORI MODELS USED TO EXAMINE VARIATION IN SURVIVAL (S) OF RADIO-MARKED NORTHERN SPOTTED OWLS AND BARRED OWLS IN WESTERN OREGON, USA, 2007–2009.

Hypothesized effects	Model ^a
Species, sex, and time effects	
Survival differs between species and among 6-month time intervals	$S(\text{Spp} \times t)$ —global model
Survival is constant between species and over time	$S(.)$ —no effects model
Survival differs between species but is constant over time	$S(\text{Spp})$
Survival differs between species and among 6-month time intervals	$S(\text{Spp} + t)$
Survival differs between species and among seasons	$S(\text{Spp} + \text{season})$
Survival differs between species and years	$S(\text{Spp} + \text{yr})$
Survival differs between species and years with an interaction	$S(\text{Spp} \times \text{yr})$
Additive effect of species and sex with constant time	$S(\text{Spp} + \text{sex})$
Interactive effect of species and sex	$S(\text{Spp} \times \text{sex})$
Additive effect of species, sex, and season	$S(\text{Spp} + \text{sex} + \text{season})$
Influence of habitat	
Survival is dependent on species and distance to edge	$S(\text{Spp} + \text{dedge})$
Interactive effect of species and distance to high-contrast edge	$S(\text{Spp} \times \text{dedge})$
Effect species and mean proportion of old forest in home range	$S(\text{Spp} + \text{old})$
Interactive effect of species and mean proportion of old forest	$S(\text{Spp} \times \text{old})$
Survival is dependent on species and mean proportion of old forest in the breeding season core-use area	$S(\text{Spp} + \text{old_core})$
Interactive effect of species and mean proportion of old forest in the breeding core area	$S(\text{Spp} \times \text{old_core})$
Additive effect of species, distance to edge, and mean proportion of old forest in the home range	$S(\text{Spp} + \text{dedge} + \text{old})$
Interactive effect of species, distance to edge, and mean proportion of old forest in breeding core area	$S(\text{Spp} + \text{dedge} + \text{old_core})$

APPENDIX D. (Continued)

Hypothesized effects	Model ^a
Influence of spatial overlap with competitors	
Survival is dependent on species and mean proportion of the home range shared with heterospecific neighbors	$S(\text{Spp} + \text{HR})$
Interactive effect of species and mean proportion of the home range shared with heterospecific neighbors	$S(\text{Spp} \times \text{HR})$
Survival is dependent on species and probability of heterospecific presence within the home range	$S(\text{Spp} + \text{PHR})$
Interactive effect of species and probability of heterospecific presence within the home range	$S(\text{Spp} \times \text{PHR})$
Combined effect of habitat and competitors	
Combine best time and sex model from 1 to 10 above with best habitat model from 11 to 18 and best interspecific model from 19 to 22	$S(\text{best from 1 to 18} + \text{best from 19 to 22})$

^a Time effects modeled as constant (.), varying between years (yr), varying among 6-month time intervals (*t*), or varying between breeding and nonbreeding seasons (season). Model covariates included owl species (Spp), proportion of old conifer forest in the home range (old), proportion of old conifer forest in the breeding core area (old_core), mean distance to high-contrast edge (dedge), proportion of home range shared with heterospecifics (HR), and probability of heterospecific presence within the home range (PHR).

APPENDIX E. RANKING OF A PRIORI MODELS USED TO CHARACTERIZE NIGHTTIME RESOURCE SELECTION BY NORTHERN SPOTTED OWLS AND BARRED OWLS IN WESTERN OREGON, USA, 2007–2009.

Model ^a	<i>K</i>	AIC	ΔAIC	AIC wt
Spotted owl (<i>n</i> = 25 owls, 42 choice sets)				
Fortype + dnest ² + slope + dstream + dHET + (HDW × dHET)	10	31,014.2	0.00	0.90
Fortype + dnest ² + slope + dstream + dHET	9	31,019.8	5.53	0.06
Fortype + dnest ² + slope + dstream + dHET + (OLD × dHET)	10	31,020.4	6.14	0.04
Fortype + dnest ² + slope + dstream + HETcore	9	31,031.3	17.07	0.00
Fortype + dnest ² + slope + dstream	8	31,045.6	31.38	0.00
Fortype + dnest ² + slope + dedge ² + dstream	10	31,046.1	31.86	0.00
Fortype + dnest ² + dstream	7	31,046.7	32.51	0.00
Fortype + dnest ² + dedge ² + dstream	9	31,047.5	33.25	0.00
Fortype + dnest ²	6	31,101.1	86.83	0.00
Fortype + dnest ² + slope	7	31,101.7	87.42	0.00
Fortype + dnest ² + dedge	7	31,101.9	87.62	0.00
Fortype + dnest ² + dedge ²	8	31,103.0	88.77	0.00
Fortype + dnest ² + slope + dedge ²	9	31,103.4	89.16	0.00
Fortype + dnest	5	31,173.1	158.84	0.00
Fortype	4	31,199.8	185.54	0.00
QMDcon + QMDcon ² + CANCOVhdw + dnest ²	5	31,249.9	235.66	0.00
QMDcon + QMDcon ² + CANCOVhdw	3	31,351.9	337.70	0.00
QMDcon + QMDcon ² + CANCOVhdw + CANCOVhdw ²	4	31,353.9	339.65	0.00
QMDcon + QMDcon ²	2	31,441.1	426.88	0.00
QMDcon	1	31,461.9	447.68	0.00
TPHcon50	1	31,584.7	570.44	0.00
CANCOVhdw + CANCOVhdw ²	2	31,889.8	875.61	0.00
CANCOVhdw	1	31,899.7	885.47	0.00
BAhdw ²	2	31,905.7	891.50	0.00
BAhdw	1	31,911.0	896.74	0.00
Null model	0	31,964.5	950.31	0.00
Barred owl (<i>n</i> = 26 owls, 43 choice sets)				
Fortype + dnest ² + slope + dedge ² + dstream	10	30,673.3	0.00	0.41
Fortype + dnest ² + slope + dedge ² + dstream + dHET + (OLD × dHET)	12	30,675.0	1.72	0.17
Fortype + dnest ² + slope + dedge ² + dstream + HETcore	11	30,675.2	1.96	0.15
Fortype + dnest ² + slope + dedge ² + dstream + dHET	11	30,675.8	2.55	0.12
Fortype + dnest ² + slope + dedge ² + dstream + dHET + (HDW × dHET)	12	30,676.5	3.23	0.08
Fortype + dnest ² + slope + dstream	8	30,677.9	4.66	0.04
Fortype + dnest ² + slope + dedge ²	9	30,679.2	5.96	0.02
Fortype + dnest ² + slope	7	30,684.6	11.30	0.00
Fortype + dnest ² + dedge ² + dstream	9	30,703.2	29.96	0.00
Fortype + dnest ² + dstream	7	30,705.9	32.59	0.00
Fortype + dnest ² + dedge ²	8	30,712.9	39.66	0.00
Fortype + dnest ² + dedge	7	30,715.1	41.82	0.00
Fortype + dnest ²	6	30,716.1	42.82	0.00
Fortype + dnest	5	30,809.5	136.27	0.00
QMD ² + CANCOVhdw ² + dnest ²	6	30,931.1	257.82	0.00
Fortype	4	31,131.8	458.48	0.00
QMDcon + QMDcon ² + CANCOVhdw + CANCOVhdw ²	4	31,375.0	701.77	0.00
QMDcon + QMDcon ² + CANCOVhdw	3	31,378.6	705.27	0.00
QMDcon + QMDcon ²	2	31,380.6	707.29	0.00
QMDcon	1	31,388.3	715.03	0.00

(Continued)

APPENDIX E. (Continued)

Model ^a	K	AIC	ΔAIC	AIC wt
TPHcon50	1	31,451.2	777.90	0.00
CANCOVhdw	1	31,622.9	949.65	0.00
CANCOVhdw + CANCOVhdw ²	2	31,623.9	950.57	0.00
BAhdw	1	31,623.9	950.64	0.00
Null model (no effects)	0	31,625.4	952.16	0.00
BAhdw ²	2	31,625.9	952.64	0.00
Species combined (n = 51 owls, 85 choice sets)				
Fortype + dnest ² + slope + dstream + dedge ² + (spp × fortype) + (spp × dnest ²) + (spp × slope) + (spp × dstream) + (spp × dedge ²)	20	61,719.4	0.00	1.00
Fortype + dnest ² + slope + dstream + dedge ² + (spp × dnest ²) + (spp × slope) + (spp × dstream) + (spp × dedge ²)	16	61,758.1	38.71	0.00
Fortype + dnest ² + slope + dstream + dedge ²	10	61,976.7	257.38	0.00
Null model (no effects)	0	63,589.9	1,870.61	0.00

^aKey to model notation: K = number of covariates in the model; AIC = Akaike's Information Criterion; ΔAIC = difference between the AIC value of each model and the lowest AIC model; AIC wt = Akaike weight. Forest type was a categorical variable with 5 levels: old conifer (OLD), mature conifer, young conifer, riparian-hardwood (HDW), and nonforest. Other model covariates included slope, distance to nest (dnest), distance to stream (dstream), distance to high contrast edge (dedge), proximity to heterospecific core-use area (dHET), area within a heterospecific neighbor's core-use area (HETcore), density of all live conifers ≥ 50 cm dbh (TPHcon50), basal area of hardwoods (BAhdw), average quadratic mean diameter of conifers (QMDcon), and canopy cover of hardwoods (CANCOVhdw).

APPENDIX F. MEAN MASS, BEHAVIORAL ATTRIBUTES, AND FREQUENCY OF OCCURRENCE (n) OF PREY SPECIES IDENTIFIED IN PELLETS OF NORTHERN SPOTTED OWLS AND BARRED OWLS IN WESTERN OREGON, USA, 2007–2009.

Prey species	Mean mass (g) ^a	Activity code ^b	Spotted owl, n	Barred owl, n
Mammals			1,133	1,446
Northern flying squirrel (<i>Glaucomys sabrinus</i>)	40–150 (3)	N, A	445	493
Deer mouse (<i>Peromyscus maniculatus</i>)	22 (1)	N, T	223	149
Red tree vole (<i>Arborimus longicaudus</i>)	26 (1)	N, A	179	155
Unidentified woodrat (<i>Neotoma fuscipes</i> or <i>N. cinerea</i>)	285 (4)	N, S	91	63
Unidentified rabbit or hare	50–900 (3)	B, T	49	54
Unidentified vole or mouse (<i>Muridae</i> spp.)	25 (4)	N, T	41	17
Western red-backed vole (<i>Myodes californicus</i>)	23 (1)	N, T	36	67
Creeping vole (<i>Microtus oregoni</i>)	20 (1)	N, T	14	54
Mountain beaver (<i>Aplodontia rufa</i>)	100–550 (3)	N, T	12	36
Douglas squirrel (<i>Tamiasciurus douglasii</i>)	221 (1)	D, S	11	89
Unidentified shrew (<i>Sorex</i> spp.)	5 (1)	N, T	10	2
Western pocket gopher (<i>Thomomys mazama</i>)	95 (1)	N, T	9	20
Trowbridge's or vagrant shrew (<i>S. trowbridgii/vagrans</i>)	5 (1)	N, T	8	375
Shrew mole (<i>Neurotrichus gibbsii</i>)	9 (1)	N, T	7	169
Vagrant shrew (<i>Sorex vagrans</i>)	5 (1)	N, T	6	34
Townsend's chipmunk (<i>Tamias townsendii</i>)	83 (1)	D, S	6	46
Pacific jumping mouse (<i>Zapus trinotatus</i>)	24 (1)	N, T	6	35
Trowbridge's shrew (<i>Sorex trowbridgii</i>)	5 (1)	N, T	4	39
Coast mole (<i>Scapanus orarius</i>)	56 (1)	N, T	4	508
Big brown bat (<i>Eptesicus fuscus</i>)	15 (1)	N, F	4	1
Unidentified bat (<i>Myotis</i> spp.)	6 (4)	N, F	2	6
Townsend's vole (<i>Microtus townsendii</i>)	54 (1)	N, T	2	14
Ermine (<i>Mustela erminea</i>)	55 (1)	N, T	2	14
Unidentified vole (<i>Microtus</i> spp.)	30 (4)	N, T	1	18
Fog shrew (<i>Sorex sonomae</i>)	9 (1)	N, T		87
Pacific marsh shrew (<i>Sorex bendirii</i>)	18 (1)	N, T		6
Townsend's mole (<i>Scapanus townsendii</i>)	130 (1)	N, T		90
Brush rabbit (<i>Sylvilagus bachmani</i>)	50–750 (3)	B, T		19
Snowshoe hare (<i>Lepus americanus</i>)	50–1,400 (3)	B, T		11
Western gray squirrel (<i>Sciurus griseus</i>)	450 (1)	D, S		6
Western spotted skunk (<i>Spilogale gracilis</i>)	606 (1)	N, T		10
Long-tailed vole (<i>Microtus longicaudus</i>)	56 (1)	N, T		9
Common muskrat (<i>Ondatra zibethicus</i>)	1,169 (1)	B, Q		3
Black rat (<i>Rattus rattus</i>)	250 (3)	N, T		1
Unidentified weasel (<i>Mustela</i> spp.)	25 (3)	N, T		54
Unidentified mammal	30–400 (3)	U, U		2
Birds			49	134
Varied thrush (<i>Ixoreus naevius</i>)	78 (2)	D, F	6	6
Steller's jay (<i>Cyanocitta stelleri</i>)	128 (2)	D, F	5	7
Northern pygmy owl (<i>Glaucidium gnoma</i>)	68 (2)	N, F	4	1
Western screech owl (<i>Megascops kennicottii</i>)	169 (2)	N, F	4	9

APPENDIX F. (Continued)

Prey species	Mean mass (g) ^a	Activity code ^b	Spotted owl, <i>n</i>	Barred owl, <i>n</i>
Pacific wren (<i>Troglodytes pacificus</i>)	9 (2)	D, F	4	27
Unidentified small bird	5–59 (3)	D, F	4	16
Golden-crowned kinglet (<i>Regulus satrapa</i>)	6 (2)	D, F	3	1
American robin (<i>Turdus migratorius</i>)	77 (2)	D, F	3	3
Gray jay (<i>Perisoreus canadensis</i>)	73 (2)	D, F	2	1
Northern flicker (<i>Colaptes auratus</i>)	142 (2)	D, F	2	4
Hairy woodpecker (<i>Picoides villosus</i>)	66 (2)	D, S	2	1
Red-breasted nuthatch (<i>Sitta canadensis</i>)	10 (2)	D, F	2	3
Northern saw-whet owl (<i>Aegolius acadicus</i>)	83 (2)	N, F	2	8
Swainson's thrush (<i>Catharus ustulatus</i>)	31 (2)	D, F	2	2
Dark-eyed junco (<i>Junco hyemalis</i>)	18 (2)	D, F	1	9
Mountain quail (<i>Oreortyx pictus</i>)	224 (2)	D, F	1	3
Unidentified warbler (<i>Setophaga</i> spp.)	8 (4)	D, F	1	1
Red-breasted sapsucker (<i>Sphyrapicus ruber</i>)	49 (2)	D, F	1	2
Band-tailed pigeon (<i>Patagioenas fasciata</i>)	392 (2)	D, F		7
Spotted towhee (<i>Pipilo maculatus</i>)	40 (2)	D, F		1
Chestnut-backed chickadee (<i>Poecile rufescens</i>)	10 (2)	D, F		4
Ruffed grouse (<i>Bonasa umbellus</i>)	514 (3)	D, F		6
Blue grouse (<i>Dendragapus obscurus</i>)	1,050 (3)	D, F		1
Unidentified grouse spp.	350 (4)	D, F		1
Pileated woodpecker (<i>Dryocopus pileatus</i>)	287 (2)	D, S		2
Western tanager (<i>Piranga ludoviciana</i>)	28 (2)	D, F		2
Unidentified flycatcher (<i>Empidonax</i> spp.)	11 (4)	D, F		1
Unidentified medium-size bird	60–299 (3)	D, F		5
Amphibians			1	389
Unidentified medium-size salamander	22–23 (3)	N, T		186
Unidentified small salamander	6–21 (3)	N, T		124
Large salamander (<i>Ambystoma</i> or <i>Dicamptodon</i> spp.)	23–114 (3)	N, T	1	55
Unidentified frog (<i>Rana</i> spp.)	30 (6)	B, Q		24
Reptiles			2	37
Garter snake (<i>Thamnophis</i> spp.)	100 (7)	D, T	1	28
Northern alligator lizard (<i>Elgaria coerulea</i>)	35 (7)	D, T		4
Western fence lizard (<i>Sceloporus occidentalis</i>)	10 (7)	D, T	1	3
Racer (<i>Coluber constrictor</i>)	77 (8)	D, T		1
Unidentified snake	200 (4)	D, T		1
Mollusks—Gastropoda			2	271
Pacific sideband snail (<i>Monadenia fidelis</i>)	10.4 (6)	B, T		149
Pleurocerid snail (<i>Juga</i> spp.)	0.02 (6)	B, Q		63
Robust lancetooth snail (<i>Haplotrema vancouverense</i>)	7 (7)	B, T	2	55
Unidentified snail	5 (4)	B, T		4
Crustaceans			1	157
Signal crayfish (<i>Pacifastacus leniusculus</i>)	23.8 (6)	B, Q	1	157
Fish				
Unidentified fish (<i>Osteichthyes</i> spp.)	51 (9)	B, Q		10
Insects, millipedes, and springtails			19	552
Unidentified ground beetle (<i>Carabidae</i> spp.)	0.3 (5)	U, U	1	300
Ground beetle (<i>Pterostichus lama</i>)	0.3 (5)	U, U	11	89
Unidentified ant (<i>Formica</i> spp.)	0.1 (5)	U, U		56
Unidentified ground beetle (<i>Pterosticus</i> spp.)	0.3 (5)	U, U		26
Weevil (<i>Dyslobus lecontei</i>)	0.3 (5)	U, U		19
Unidentified small insect	0.3 (5)	U, U	1	18
Tiger beetle (<i>Omus audouini</i>)	0.3 (5)	U, U		9
Carpenter ant (<i>Camponotus</i> spp.)	0.1 (5)	U, U		9
Yellow-spotted millipede (<i>Harpaphe haydeniana</i>)	0.4 (5)	U, U		8
Ponderous borer (<i>Ergates spiculatus</i>)	2.4 (5)	U, S	5	6
Stink bug (<i>Hemiptera</i> spp.)	0.3 (5)	U, U		5
Unidentified bee (<i>Hymenoptera</i> spp.)	0.1 (5)	U, U	1	3
Ichneumon wasp (<i>Ichneumonid</i> spp.)	0.1 (5)	U, U		1
Braconid wasp (<i>Braconidae</i> spp.)	0.1 (5)	U, U		1
Unidentified large insect	2.0 (5)	U, U		1
Unidentified springtail (<i>Entomobryid</i> spp.)	0.1 (5)	U, U		1
Totals			1,246	4,306

^a Source of mass estimate is in parentheses: 1 = Verts and Carraway (1998); 2 = Dunning (1993); 3 = mass of each individual estimated based on comparison with reference specimen of known mass; 4 = mean of all species in group; 5 = mass based on estimates from similar species in this genus or group; 6 = estimated from local specimens; 7 = Forsman et al. (2004), 8 = Steenhof (1983), 9 = Behnke (2002).

^b Following Forsman et al. (2004), first letter indicates primary period of activity (D = diurnal, N = nocturnal, B = active both day and night, U = unknown), second letter indicates primary area of activity (T = terrestrial, A = arboreal, S = semi-arboreal, F = flying or aerial animal, Q = aquatic, U = unknown).

APPENDIX G. RANKING OF A PRIORI MODELS USED TO EXAMINE VARIATION IN SURVIVAL (S) OF RADIO-MARKED NORTHERN SPOTTED OWLS ($n = 29$) AND BARRED OWLS ($n = 28$) IN WESTERN OREGON, USA, 2007–2009.

Model ^a	K	AIC _c	Δ AIC _c	AIC _c wt	Deviance
$S(\text{Spp} + \text{old} + \text{PHR})$	4	89.57	0.00	0.32	81.35
$S(\text{Spp} + \text{old})$	3	89.60	0.03	0.32	83.47
$S(\text{Spp} + \text{dedge} + \text{old})$	4	91.64	2.07	0.12	83.42
$S(\text{Spp} \times \text{old})$	4	91.68	2.11	0.11	83.47
$S(\text{Spp})$	2	95.77	6.20	0.01	91.71
$S(\text{Spp} + \text{old_core})$	3	95.93	6.36	0.01	89.80
$S(\text{Spp} + \text{PHR})$	3	96.00	6.43	0.01	89.87
$S(\cdot)$ —intercept only	1	96.09	6.52	0.01	94.07
$S(\text{Spp} + \text{dedge})$	3	96.97	7.40	0.01	90.84
$S(\text{Spp} + \text{HR})$	3	97.02	7.45	0.01	90.89
$S(\text{Spp} + \text{dedge} + \text{old_core})$	4	97.27	7.69	0.01	89.05
$S(\text{Spp} + \text{season})$	3	97.36	7.79	0.01	91.23
$S(\text{Spp} + \text{sex})$	3	97.66	8.09	0.01	91.53
$S(\text{Spp} + \text{yr})$	3	97.83	8.26	0.01	91.70
$S(\text{Spp} \times \text{old_core})$	4	98.01	8.44	0.00	89.79
$S(\text{Spp} \times \text{PHR})$	4	98.03	8.46	0.00	89.81
$S(\text{Spp} \times \text{sex})$	4	98.56	8.99	0.00	90.34
$S(\text{Spp} \times \text{dedge})$	4	98.98	9.41	0.00	90.77
$S(\text{Spp} \times \text{HR})$	4	99.10	9.53	0.00	90.88
$S(\text{Spp} + \text{season} + \text{sex})$	4	99.26	9.69	0.00	91.04
$S(\text{Spp} \times \text{yr})$	4	99.79	10.22	0.00	91.58
$S(\text{Spp} + t)$	5	101.55	11.98	0.00	91.22
$S(\text{Spp} \times t)$ —global model	8	104.85	15.28	0.00	88.05

^a Key to model notation: K = number of covariates in the model; AIC = Akaike's Information Criterion; Δ AIC = difference between the AIC value of each model and the lowest AIC model; AIC wt = Akaike weight. Time effects modeled as constant ($\cdot$), varying between years (yr), varying among categorical 6-month time intervals (t), or varying in an even-odd fashion between breeding (1 Mar–31 Aug) and nonbreeding (1 Sep–28 Feb) seasons (season). Covariates included owl species (spp), proportion of old conifer forest in the home range (old), proportion of old conifer forest in the breeding season core area (old_core), mean distance to high-contrast edge (dedge), proportion of home range shared with neighboring heterospecifics (HR), and probability of heterospecific presence within the home range (PHR).