

A Briefing Paper on the Science Directly Related to the Effects of  
Barred Owls (*Strix varia*) on Spotted Owls (*Strix occidentalis*)

[Prepared for the Western Klamath Restoration Partnership]

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Barred Owls (*Strix varia*) and Spotted Owls (*Strix occidentalis*) are both large, forest-dwelling avian predators. Although both Barred and Spotted Owls rely on forested landscapes, the Barred Owl exhibits a more diverse diet – consuming mammals, birds, fish, amphibians, reptiles, and invertebrates (Mazur and James 2000) – compared to Spotted Owls that specialize on mammalian prey (Gutiérrez et al. 1995, Hamer et al. 2001, Wiens et al. 2014). Unlike the Barred Owl, the Spotted Owl is emblematic of controversy surrounding their dwindling numbers, protected status, and reliance on economically-valuable timberlands (Bart and Forsman 1992, Keane 2017). Because Barred Owls exert a disproportionately negative influence on Spotted Owl fitness where the two species co-occur, the continuing expansion of Barred Owls into the range of the Northern and California Spotted Owl has presented emergent and difficult challenges for wildlife managers.

In this report, we aimed to summarize the existing published research on Barred Owls within the range of the Spotted Owl as well as identify future research priorities. Broadly, we provide synthesized information for researchers and managers to help develop strategies focused on mitigating the deleterious effects of Barred Owl expansion in western North America.

### **Westward Expansion of the Barred Owl**

Before the second half of the last century, the ranges of the Spotted Owl and Barred Owl did not overlap. The Spotted Owl occupied the western edge of North America (Gutiérrez et al. 1995) and the Barred Owl occupied the eastern edge (Mazur and James 2000), where the Great Plains divided the two species. Barred Owls began to expand their range across the midwestern United States and central Canada in the early part of the last century (Livezey 2009a). There are several non-mutually exclusive hypotheses regarding what led to this westerly expansion, including: climate change resulting in warmer weather (Johnson 1994, Monahan and Hijmans 2007), changes in the Great Plains such as increased woody development in the form of tree plantings for shelterbelts and fire control (Knopf 1994, Livezey 2009a, 2009b), and other habitat manipulations (Root and Weckstein 1994).

After crossing central North America, the Barred Owl expanded its range into the Pacific Northwest where the first individual was observed in Alberta in 1912 (Boxall and Stepney 1982), British Columbia

in 1943 (Grant 1966), eastern Washington 1966 (Rogers 1966), western Washington 1986 (Sharp 1989), Oregon 1974 (Taylor and Forsman 1976), northwestern California 1982 (Evens and LeValley 1982), and as far south as Marin County in California by 2002 (Jennings et al. 2011) and the Sierra Nevada Mountains in eastern California in 1991 (Dark et al. 1998). The western Barred Owl range now overlaps the range of the Northern Spotted Owl (*S. o. caurina*) (Livezey 2009a) and the California Spotted Owl (*S. o. occidentalis*).

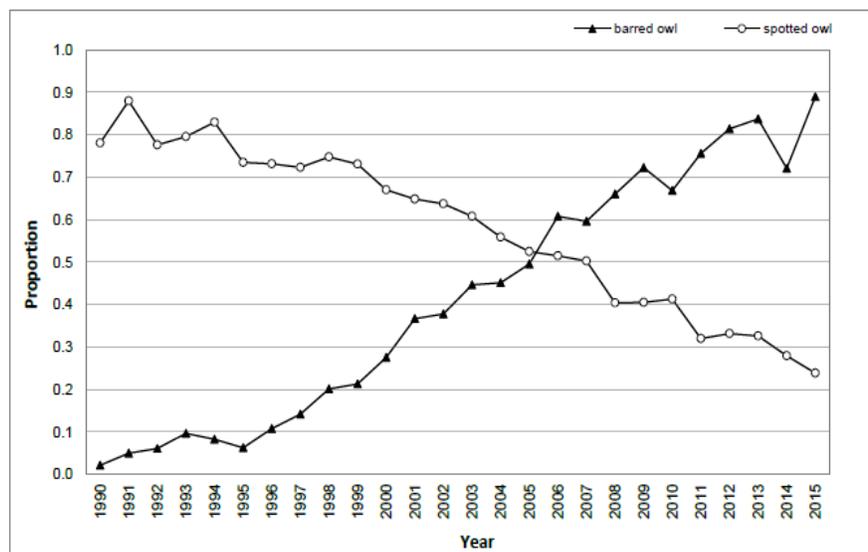
The Barred Owl has yet to expand into the range of the California Spotted Owl in the densities seen in the Northern Spotted Owl range (Keane 2017). As of 2013, 51 Barred Owls and 27 hybrids had been detected in the Sierra Nevada range, though none in the coastal or southern California parts of their range. Barred Owl numbers remain relatively low in the California Spotted Owl range when compared to the Northern Spotted Owl range, though contemporary survey efforts for Barred Owls remain incidental (Keane 2017).

### Barred Owl influence on Spotted Owl habitat use and selection

As Barred Owls expanded their range across western North America, their newly established populations in British Columbia, Washington, Oregon, and northern California continued to grow (Dark et al. 1998, Davis et al. 2016, Jones and Kroll 2016, Kelly et al. 2003, Pearson and Livezey 2003). Pervasive expansion and population growth continued until only a few isolated areas in the range of the Northern Spotted Owl remained without Barred Owls (Kroll et al. 2016). Barred Owl expansion eventually reached a critical threshold in many parts of the northern Spotted Owl range: the number of territorial Barred Owls surpassed Spotted Owl territories (Fig. 1, Lesmeister et al. 2016).

To date, few studies have tried to estimate Barred Owl population size. In one such case, Kelly (2001) estimated there were a total of 706 Barred Owl territories in Oregon by 1998, slightly more than 20 years after the first Barred Owl was recorded in Oregon in 1974 (Fig. 2). However, Gutiérrez et al. (2004) stated that detection methods which reported cumulative detections may lead to over estimates of Barred Owl populations. On the other hand, Gutiérrez et al. (2004)

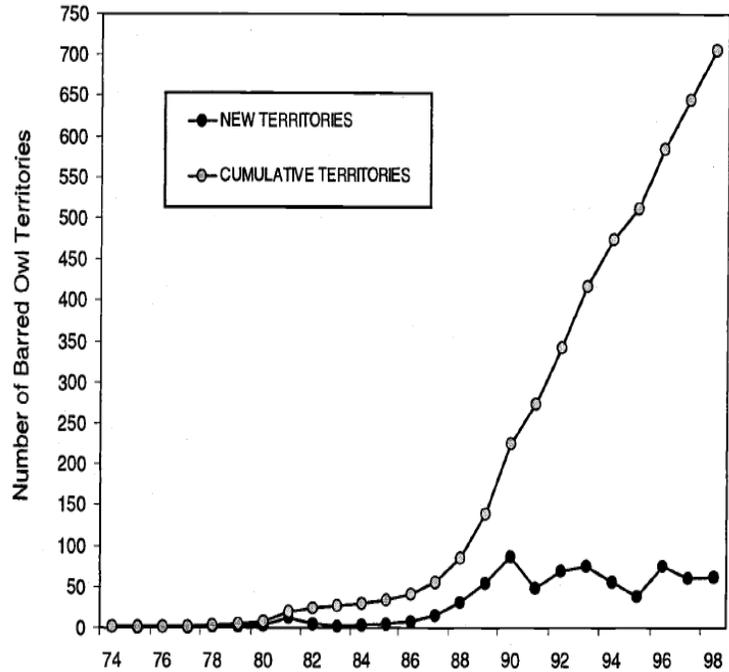
also stated that most Barred Owl sightings are reported incidentally during Spotted Owl surveys, suggesting that they may be more abundant than estimated. A new modelling framework developed by



**Figure 1.** Proportion of Spotted Owl sites in which Barred Owls and Spotted Owls were detected on the Oregon Coast Ranges Study Area, 1990–2015. From Lesmeister et al. (2016).

Zipkin et al. (2017) has leveraged these detection-nondetection data along with count data to estimate population dynamics, abundance, and individual detection probabilities from sampling Barred Owls in the Oregon Coast Ranges. They estimated that the mean site-specific number of 0.13 territorial Barred Owls in 1995 increased to 7.5 owls in 2016, with survival probabilities of 0.86-0.93 and an increased colonization rate of 0.14 in 1996 to 0.90 in 2016. Developing and implementing Barred Owl surveys would represent an important step towards fully understanding how environmental variation affects Barred Owl population growth (Wiens et al. 2011).

Both Barred and Spotted owls utilize old-growth forests. While four researchers found no differences between species' use of different age classes and composition of forests (Buchanan et al. 2004, Pearson and Livezey 2007, Singleton 2015, Singleton et al. 2010), others found Spotted Owls use older forests at greater frequencies than Barred Owls. For example, Hamer et al. (2007) reported that the home ranges of Spotted Owls in Washington were negatively influenced by the lack of old forest, that is, home ranges with less old forest were larger, indicating Spotted Owls may increase their range to increase amount of old forest in their territory. This was only slightly true for Barred Owls. Also in Washington, Herter and Hicks (2000) found that Spotted Owl territories contained more mature coniferous forests than Barred Owl territories and Pearson and Livezey (2003) found the mean age of forest stand at a site-center was significantly greater for Spotted Owls ( $254.7 \pm 76.5$  yr) than for Barred Owls ( $228.3 \pm 101.5$  yr). In Oregon, Wiens et al. (2014) found that both species used patches of old (>120 yr) coniferous forest in proportions two to three times greater than available in the study area (**Table 1**). In northern California, Weisel (2015) examined the owls' use of the understory components of the coastal redwood ecosystem and found that both Northern Spotted Owls and Barred Owls selected habitats with understory vegetation, hardwood trees, and close to their nest sites; however, Barred Owls were more likely to select foraging habitat that contained a greater percentage of hardwoods than Spotted Owls only up to a certain volume, when the stand becomes too dense to support successful foraging, suggesting that Spotted Owls are better able to utilize dense understory for foraging. Similarly, Irwin et al. (2017) found that Barred Owls selectively hunted for prey near streams at low elevations, often within hardwood-dominated stands, but use decreased with increasing densities of small-diameter trees.



**Figure 2.** Estimated number of new and cumulative Barred Owl territories reported each year in Oregon, 1974-1998. From Kelly (2001).

Environmental condition	Spotted owl				Barred owl				Random (n = 11, 974)	
	Foraging (n = 25)		Roosting (n = 16)		Foraging (n = 26)		Roosting (n = 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 <sup>2</sup> /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

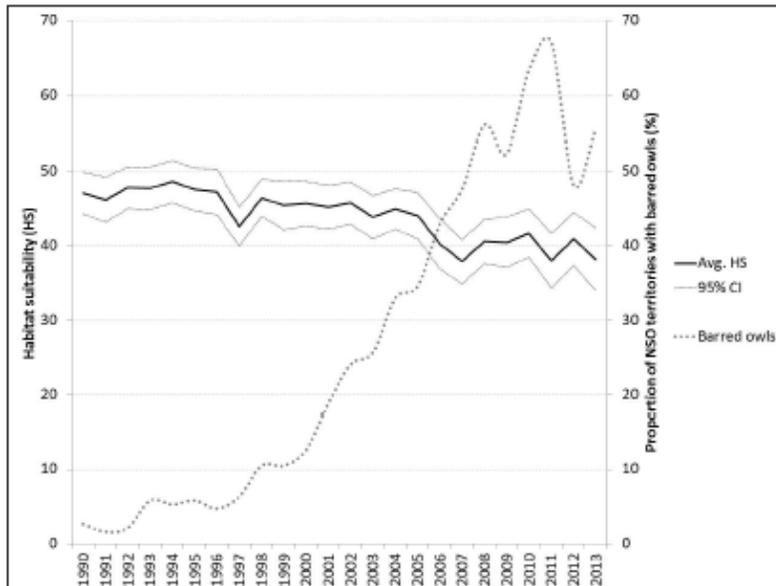
**Table 1.** Mean values of environmental conditions measured at foraging and roosting locations used by individual Spotted Owls or Barred Owls as compared to a set of random locations plotted in the western Oregon study area, USA, 2007–2009. Forest types are expressed as the mean percentage of total foraging, roosting, or random locations. We show sample sizes (number of individual owls or random points) in parentheses. From Wiens et al. (2014).

Habitat around nest sites in the Cascades were found to be similar between the species (Buchanan et al. 2004, Pearson and Livezey 2003). However, Buchanan et al. (2004) found differences in nest trees and nest configurations selected by each species. In Washington, Spotted Owls almost always placed nests in Douglas-firs (*Pseudotsuga menziesii*) (9 of 10 nests), while Barred Owls used five different tree species, including three black cottonwoods (*Populus trichocarpa*), three Douglas-firs, and two grand firs (*Abies grandis*) (Buchanan et al. 2004). Most of the trees used by Spotted Owls were alive and intact (7 of 10) while eight trees used by Barred Owls had broken boles (six alive, two dead). Also, Spotted Owls primarily used platform nests consisting of clumps of branches or goshawk nests (8 of 10), while Barred Owls used cavities or sites with chimney-like structures. Allen (1987) noted that Barred Owls in the east required large, decadent trees with cavities for nesting, though Livezey (2007) found 25% used other locations such as hawk nests, tops of hollow trees, and squirrel nests throughout their range.

Barred Owls appear to have a negative effect on the Spotted Owl's ability to utilize preferred habitat. For example, Davis et al. (2016) modeled habitat suitability in the Tyee density study area in Oregon and found a strong negative correlation ( $r = -0.894$ ) between an increasing trend of Spotted Owl territories with Barred Owls and the average Habitat Suitability Index. The 2013 index was significantly lower than it was in 1990 when Barred Owls occurred in low numbers (**Fig. 3**). Pearson and Livezey (2003) found that Late Successional Reserves (LSRs) in Washington were getting more use by Barred Owls than Spotted Owls for whom they were set aside. They found 34% more Barred Owl sites than Spotted Owl sites in LSRs, while there were 33% more Spotted Owl than Barred Owl sites in non-LSR lands.

The greatest difference in habitat use between Spotted and Barred Owls is an apparent dissimilar use of topographies by the two species: Spotted Owls used steeper, higher-elevation sites while Barred Owls used flatter, low-elevation sites – sometimes along streams (Hamer et al. 2007, Herter and Hicks 2000, Pearson and Livezey 2003, 2007, Wiens et al. 2014) (**Table 1**). Pearson and Livezey (2007) found that elevation and slope were important factors in explaining densities of Spotted Owls in Washington, when combined with measures of forest quality, forest age, distance to water, and abundance and availability of prey. They posited that the persistence and higher numbers of Spotted Owls in one LSR, despite the

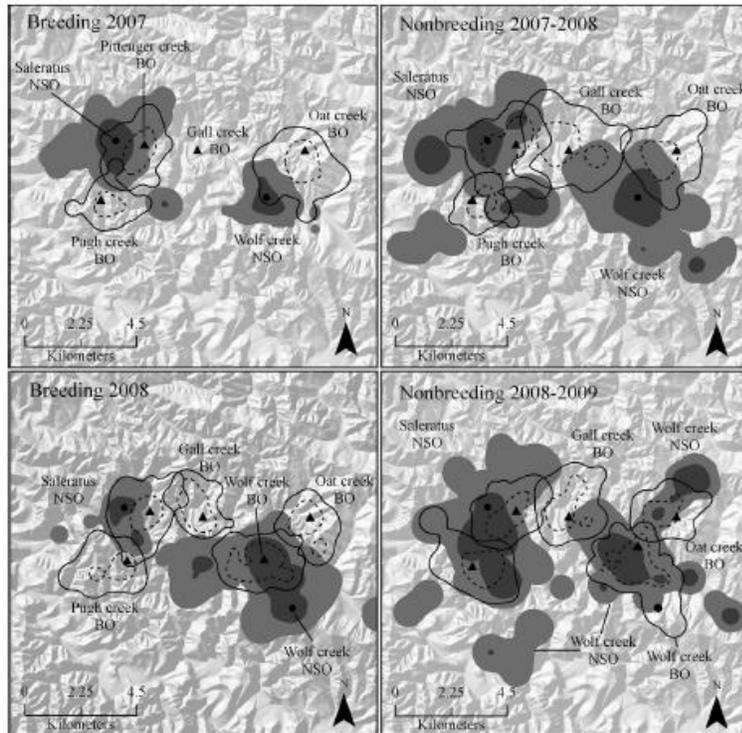
invasion of Barred Owls in other LSRs, may indicate that there are local environmental factors such as elevation and slope that favor Spotted Owls over Barred Owls, and that a natural balance had been achieved in their study area which allowed the coexistence of these two species.



**Figure 3.** Relationship between Barred Owl presence and Northern Spotted Owl (NSO) habitat selection. From Davis et al. (2016).

### **Influence of Barred Owls on Spotted Owl Occupancy, Survival, and Fecundity**

As Barred Owl populations increase, they can either form new territories in Spotted Owl territories without displacing Spotted Owls (Wiens et al. 2014), actively displace resident Spotted Owls from their territories (Dugger et al. 2011, Kelly et al. 2003, Pearson and Livezey 2003, Sharp 1989), or reduce Spotted Owl occupancy rates (Kelly et al. 2003, Kroll et al. 2010, Pearson and Livezey 2003). When Barred Owls establish territories inside Spotted Owl territories, some Barred Owl territories may be contained entirely within Spotted Owl territories (**Fig. 4**), since the estimated size of Spotted Owl territories can be more than six times the size of Barred Owl territories (**Table 2**) (Hamer et al. 2007, Wiens 2012, Wiens et al. 2014). Wiens et al. (2014) found that each individual Spotted Owl shared a portion of its home range, usually foraging areas, with 0-8 Barred Owls in adjacent territories (average = 2.4 Barred Owls per Spotted Owl). Spotted Owls were less likely to use an area if it was within or near a core-use area of a Barred Owl (Wiens et al. 2014). By contrast, in coastal northern California, Weisel (2015) found no significant difference in average home range size between the two species in either the breeding or non-breeding seasons, however Spotted Owl territories tended to be slightly larger (**Table 2**).



**Figure 4.** 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. From Wiens et al. (2014).

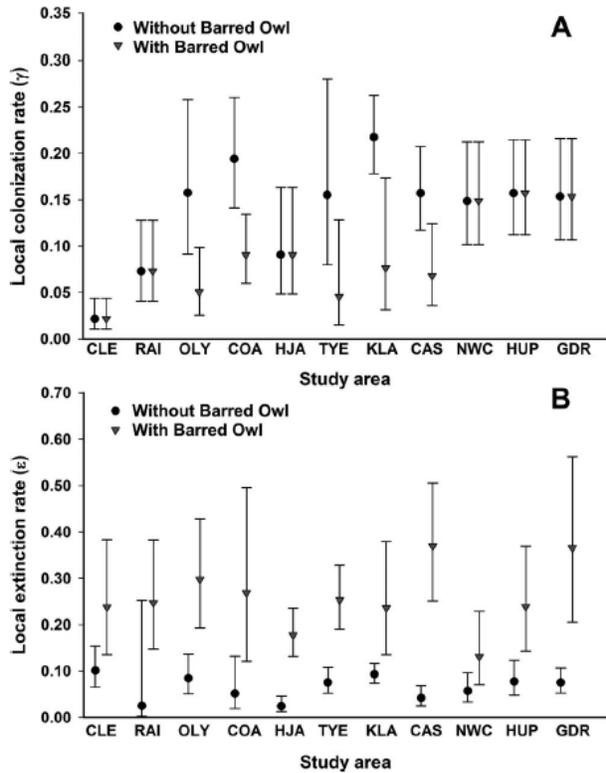
One of the earliest incidents of “displacement” of a Spotted Owl by a Barred Owl was recorded in Washington state by Sharp (1989). In 1985, Sharp recorded the first Barred Owls on the Olympic Peninsula. The following year, two Barred Owl pairs had apparently displaced two Spotted Owl pairs from their territories.

The presence of Barred Owls yields a measurable effect on Spotted Owl colonization and extinction rates. Five of the six studies that estimated colonization probabilities found a negative effect of Barred Owls on colonization, though it was sometimes weak (Dugger et al. 2011, 2016; Kroll et al. 2010; Olson et al. 2005; Yackulic et al. 2014). Sovern et al. (2014) found no effects of Barred Owls on colonization rates. Dugger et al. (2016) found the presence of Barred Owls resulted in a lower local colonization rate in five of eleven study areas in the Northern Spotted Owl range (**Fig. 5A**). Also, Yackulic et al. (2014) found that two of their top four models for their Tye study area suggested that Spotted Owls were less likely to colonize an area that was already occupied by Barred Owls, while, conversely, Barred Owls were more likely to colonize areas already occupied by Spotted Owls. Dugger et al. (2011) found that Barred Owls displaced Spotted Owls from historical breeding territories in southern Oregon, as Spotted Owl site occupancy was lower where Barred Owls were detected as compared to sites where Barred Owls were not detected (**Fig. 6**). Similarly, Kelly et al. (2003) found that mean annual Spotted Owl occupancy declined after Barred Owls were detected within 0.80 km of territory centers in Oregon and Washington, as compared to Barred Owl-absent territories. Pearson and Livezey (2003) noted about 20% of 129 Spotted Owl sites surveyed from 1996-2001 were unoccupied by Spotted Owls by 2001 in southwestern Washington; they determined there were significantly more Barred Owl site-centers in unoccupied than occupied Spotted Owl home range circles. Kroll et al. (2010) documented lower Spotted Owl occupancy probabilities when Barred Owls were present throughout their study sites in eastern Washington.

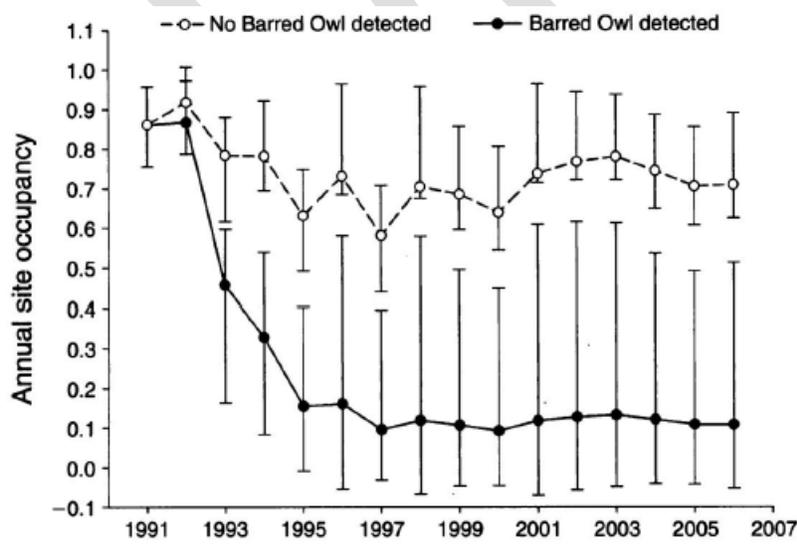
Study	Area	Season	Territory size - All		Territory size - Females		Territory size - Males	
			Spotted Owl	Barred Owl	Spotted Owl	Barred Owl	Spotted Owl	Barred Owl
Hamer et al. 2007	Baker Lake, WA	annual	2659 ± 626	781 ± 216	3517 ± 1091	527 ± 51	1706 ± 392	1184 ± 545
Hamer et al. 2007	Baker Lake, WA	summer	1505 ± 288	299 ± 30	1783 ± 464	299 ± 33	1199 ± 321	300 ± 58
Hamer et al. 2007	Baker Lake, WA	winter	2920 ± 868	950 ± 268	2954 ± 857	579 ± 75	2875 ± 1714	1488 ± 631
Singleton et al. 2010	Eastern Cascades, WA	annual				416 ± 250		477 ± 194
Singleton et al. 2010	Eastern Cascades, WA	breeding				202 ± 35		183 ± 67
Singleton et al. 2010	Eastern Cascades, WA	nonbreeding				322 ± 253		429 ± 190
Wiens 2012	Central Cascades, OR	annual	2813 ± 290	879 ± 110	3165 ± 490	737 ± 77	2507 ± 332	1015 ± 201
Wiens 2012	Central Cascades, OR	breeding	1620 ± 193	556 ± 41	1508 ± 288	487 ± 57	1712 ± 265	614 ± 57
Wiens 2012	Central Cascades, OR	nonbreeding	2688 ± 273	1028 ± 139	3008 ± 450	874 ± 114	2351 ± 292	1168 ± 243
Schilling et al. 2013	Klamath Mountains, OR	annual	576 ± 75		511		630	
Schilling et al. 2013	Klamath Mountains, OR	breeding	491 ± 97					
Schilling et al. 2013	Klamath Mountains, OR	nonbreeding	469 ± 59					
Weisel 2015	North Coast Range, CA	breeding	391 ± 79	303 ± 37				
Weisel 2015	North Coast Range, CA	nonbreeding	560 ± 159	442 ± 97				

**Table 2.** Home range sizes (mean ha ± SE) for Northern Spotted Owls and Barred Owls in Washington, Oregon, and northern California. Hamer et al. (2007) estimates were calculated using 95% Adaptive Kernel Method, all others used 95% Fixed Kernel Method.

Spotted Owl extinction probabilities increased when Barred Owls were present in all six studies for which they were estimated (Dugger et al. 2011, 2016; Kroll et al. 2010; Olson et al. 2005; Sovern et al. 2014, Yackulic et al. 2014). Dugger et al. (2016) found higher extinction rates for the Northern Spotted Owl in all study areas in its range when Barred Owls were present (**Fig. 5B**). Olson et al. (2005) noted that the increase in local extinction probabilities affected occupancy probabilities, leading to occupancy rate declines of up to 15% for Spotted Owls. When the two species were modelled together, Yackulic et al. (2014) found that extinction probabilities increased for each species when the other was present, suggesting a strong role of competition in occupancy dynamics.



**Figure 5.** Mean (A) local colonization and (B) extinction rates with 95% confidence intervals for Northern Spotted Owls in 11 study areas in Washington, Oregon, and California, USA, 1985–2013, relative to when a territory was also occupied by Barred Owls (gray triangles) and when Barred Owls were not present (black circles). Estimates reflect mean values for other factors in the best model for each study area. Data from the Barred Owl removal treatment areas in the GDR study area were excluded after 2008, so that all study areas were comparable. See Appendix A for study area abbreviations. From Dugger et al. (2016).



**Figure 6.** Estimates of mean annual site occupancy generated across all Northern Spotted Owl territories in southern Oregon from 1991 to 2006. From Dugger et al. (2011).

Simulations have yielded concordant results. For example, Yackulic et al. (2014) found a strong role of intraspecific competition in structuring occupancy dynamics in their modelling. Their simulations suggested competition has a much more substantial impact on the equilibrium occupancy values of Spotted Owls than that of Barred Owls. These simulations also suggest that competition at the patch scale led to increased rates of local extinction for Spotted Owls and, though this would probably not directly drive competitive exclusion from territories, it would result in reduced equilibrium occupancies. Dugger et al. (2011) noted that the strong negative effect of the Barred Owl on occupancy dynamics of Northern Spotted Owls provided evidence of interference competition. By contrast, Bailey et al. (2009) modeled the co-occurrence of Spotted and Barred owls using a two-species occupancy model and found no evidence that Barred Owls excluded Spotted Owls from territories. However, the two species co-occurred less often than expected. Multiple field studies coupled with simulations demonstrate that interspecific competition occurs between Barred and Spotted Owls which has led to reduced colonization coupled with heightened extinction probabilities of Spotted Owls.

Studies that examined the effect of Barred Owls on Northern Spotted Owl fecundity and recruitment have produced mixed results. Three of six studies showed no effect of the presence of Barred Owls on Spotted Owl fecundity (measured as number of young fledged per female per year; Anthony et al. 2006, Dugger et al. 2016, Iverson 2004). The other three studies showed a negative, though not always strong, effect (Glenn et al. 2010, 2011b; Olson et al. 2004). Glenn et al. (2010) found that Spotted Owl recruitment rates were diminished in the presence of Barred Owls in four of six study areas. This mixed result may point to other factors influencing fecundity, for instance Wiens (2012) found that the number of young fledged by Spotted Owls increased linearly with increasing distance from the nearest Barred Owl nest or territory center. When Spotted Owl young fledged, Barred Owl detections had no direct relationship with natal or settling locations or dispersal distances (Hollenbeck et al. 2018). They also found that net dispersal distances varied by ecoregions (Washington Coast and Cascades, Washington Eastern Cascades, Oregon Coast Range, Oregon and California Cascades, and Oregon and California Klamath) but declined similarly in all ecoregions over time (~1 km/yr).

Spotted Owl survival was mostly negatively affected by the presence of Barred Owls. Of six studies that analyzed apparent or actual survival, two showed definite negative effects of Barred Owl presence on Northern Spotted Owl survival estimates (Dugger et al. 2016, Glenn et al. 2010), three showed weak negative effects (Anthony et al. 2006, Glenn et al. 2011a, Wiens 2012), and one showed no effect (Schilling et al. 2013).

## Diet

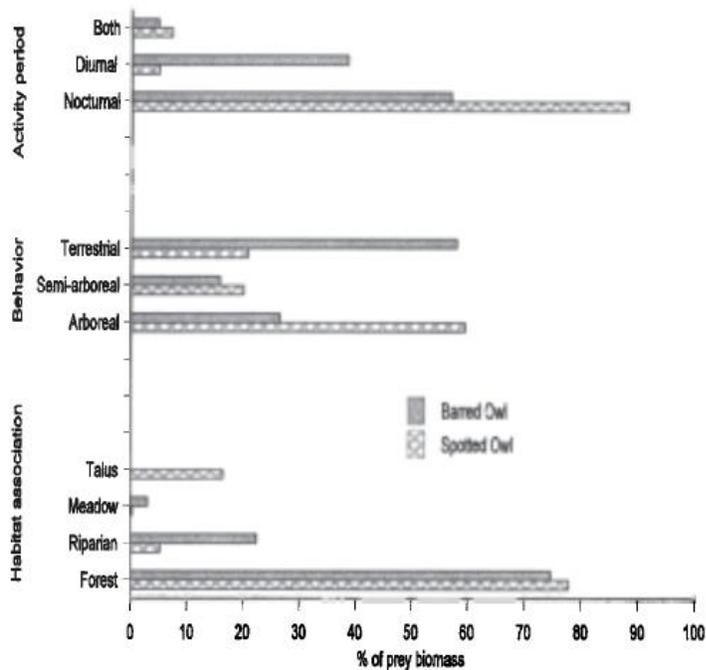
Spotted and Barred owl diets overlap to some degree in all regions. Hamer et al. (2001) and Wiens et al. (2014) used the Pianka Index to estimate a dietary overlap of 76% in the western Cascades Range in Washington and 44.6% in the central Coast Range in Oregon, respectively. In both studies, Spotted Owl diets were heavily dependent on mammals, which were about 95% of the prey items consumed, especially Northern flying squirrels (*Glaucomys sabrinus*); and while more than half of Barred Owl diets depended on mammals including the Northern flying squirrel, they also included a greater percentage of smaller mammals like shrews (*Sorex* and *Neurotrichus* spp.) and moles (*Scapanus* spp.), as well as birds, amphibians, and arthropods (**Table 3**).

Barred Owl diets also varies between regions, demonstrating a broad range in prey. Graham (2012) examined Barred Owl pellets from three study areas: Olympic National Forest and the eastern Cascades in Washington, and the Central Coast Range in Oregon. He found that their diet was considerably different between the two western mountain range study areas and the eastern Cascade Range, which is considerably drier and hotter (**Table 3**). In the eastern mountains, Barred Owls did not depend as much on mammals which was only 26.5% of their diet, but instead relied more on arthropods (47%), as well as amphibians and reptiles (11.1%). Livezey et al. (2008) found that Barred Owls will also eat soft-bodied prey such as earthworms and slugs, which would not be easily detected in regurgitated pellets, upon which these studies depended.

Prey	Spotted Owl		Barred Owl				
	Hamer et al. 2001	Wiens et al. 2014*	Hamer et al. 2001	Wiens et al. 2014*	Graham 2012		
	Western Cascades, WA	Central Coast Range, OR (n = 16)	Western Cascades, WA	Central Coast Range, OR (n = 25)	Central Coast Range, OR (n = 3,463)	Olympic NP, WA (n = 187)	Eastern Cascades, WA (n = 336)
Mammals	96.2	94.2	76.1	63.5	63.4	71.7	26.5
Moles, shrews	4.0	3.0	23.8	31.4	32.2	34.1	5.1
Lagomorphs	3.0	3.8	8.3	1.9	1.4	0.5	1.2
Northern flying squirrel	50.7	36.5	20.0	11.0	10.3	15.5	12.2
Douglas squirrel	1.7	0.9	8.3	2.0	2.0	2.1	1.5
Deer mouse	20.6	18.2	6.8	3.5	4.0	3.7	1.5
Woodrats	4.4	7.2	0.0	1.4	1.3	0.0	0.3
Red tree vole	0.0	14.2	0.0	3.5	3.9	0.0	0.0
Birds	2.8	4.0	11.0	3.0	2.7	6.4	3.6
Fish	0.0	0.0	4.0	0.2	0.2	0.5	0.0
Amphibians,	0.0	0.1	15.0	9.1	11.1	7.5	22.9
Arthropods	1.0	<0.1	10.0	15.0	15.0	10.7	47.0
Gastropods	0.0	<0.1	2.0	6.9	6.8	3.2	0.0

**Table 3.** Select Barred Owl and Spotted Owl prey items found in regurgitated pellets from three studies in Washington and Oregon. Percent of total number of items identified in owl pellets are listed, with number of pellets sampled in parentheses. No sample size was reported from Hamer et al. (2001).

Spotted and Barred owls can select different prey based on the prey's activity period, behavior, and habitat associations. In western Washington, Hamer et al. (2001) found that Spotted Owls most often selected nocturnal and arboreal species, and those inhabiting forest and talus habitats (**Fig. 7**). By contrast, Barred Owls selected more diurnal and terrestrial species, and those in forest, meadow, and riparian habitats. They did not select any talus species.



**Figure 7.** Diets (% of total biomass) of Northern Spotted Owls and Northern Barred Owls in western Washington, subdivided based on habitat associations, behavior types and primary activity period of prey. From Hamer et al. (2001).

Barred Owls are known to be predators of other owl species, including *Strix* species on rare occasions (Graham 2012, Wiens 2012). Graham found the remains of two unidentified *Strix* species near Barred Owl roost trees or nests. Wiens found the remains of two Spotted Owls cached beneath fallen logs with wounds consistent with those inflicted by a large raptor. He was unable to rule out they were not killed by Barred Owls, since Great Horned Owls (*Bubo virginianus*) were also in the vicinity. Leskiw and Gutiérrez (1998) found a freshly dead Spotted Owl that may have been killed by a Barred Owl. The Barred Owl that flew in next to the authors in response to a Spotted Owl call had feathers similar to those of a Spotted Owl in its talons.

## Behavior

When Spotted and Barred owls interact, the Barred Owl most frequently assumes the dominant role (Van Lanen et al. 2011). Van Lanen et al. conducted experiments using playback tapes and mounted owl taxidermy mounts for both species. They found that male Barred Owls gave more aggressive calls and were more likely to attack the Spotted Owl mount, while male Spotted Owls were less likely to give aggressive calls or attack the Barred Owl mount. Gutiérrez et al. (2004) reported instances where Barred Owls have attacked Spotted Owls, as well as surveyors imitating Spotted Owl calls. Wiens (2012) reported regular interspecific territorial interactions between newly colonizing Barred Owls within the breeding home ranges of Spotted Owls. Interactions included agitated vocalizations by both species near nest sites and Barred Owls chasing Spotted Owls out of shared core-use areas (but not the opposite). In California, Jennings et al. (2011) reported a Barred Owl chasing a female Spotted Owl.

Conversely, there are few observations of Spotted Owl aggressions towards Barred Owls, with the exception of a few reports of nesting Spotted Owls defending a nest or a family group (Gutiérrez et al. 2004) and Jennings et al.'s (2011) report of a pair of Spotted Owls charging and diving at a Barred Owl

and an “aerial clash” between a Spotted and Barred Owl (though they did not report how that interaction started).

Crozier et al. (2006) reported that both California and Northern Spotted Owls responded less frequently to Spotted Owl calls after exposure to Barred Owl calls and Northern Spotted Owls responded less frequently in areas having higher numbers of Barred Owls. Other researchers have also noted that the presence of Barred Owls adversely affected Spotted Owl detectability (Bailey et al. 2009, Crozier et al. 2006, Kroll et al. 2010, Olson et al. 2005, Sovern et al. 2014). Olson et al. (2005) found the presence of Barred Owls was important for modeling detectability among years in all occupancy analyses, having a negative effect on Spotted Owl detectability. However, Gutiérrez et al. (2004) noted that even if this were the case, there does not appear to be a decline in Spotted Owl recapture rates, which he stated would be expected if Barred Owls were causing significant behavioral interference.

In consideration of the potential for modified Spotted Owl behavior in the presence of Barred Owls, Wasser et al. (2012) demonstrated an alternate method for surveying both owl species. Their method uses trained “detection dogs” to search out accumulated owl pellets under roost sites, then analyzing the mitochondrial DNA in the pellets to confirm species. The researchers found that detection probabilities using this method were significantly higher for both species than with standard vocalization surveys.

### **Hybridization between Spotted and Barred Owls**

The first Spotted Owl x Barred Owl hybrids were reported in 1987 (Kelly 2001, Kelly and Forsman 2004). Since then, at least 50 hybrids have been reported in the Northern Spotted Owl’s range (Hamer et al 1994, Mazur and James 2000, Pearson and Livezey 2003, Seamans et al. 2004). Kelly and Forsman (2004) reported the very low rate of interspecific matings, thereby suggesting that the rate of hybridization will likely not be a serious threat to the Spotted Owl. However, they also stated, it is possible that hybridization is more common than reported since hybrid backcrosses are hard to identify in all cases. Funk et al. (2007) found that of 12 owls identified as hybrids by plumage in the field, five (almost half) were either Barred (3) or Spotted (2) owls by genetic testing. Hanna et al. (2018) suggested that if hybridization does become more frequent, genetic swamping of the Northern Spotted Owl may occur leading to genetic introgression, which could reduce fitness; however he found no evidence of introgression. Forensic genetic investigation shows that the two species show extensive evolutionary divergence, and that the hybrids are primarily crosses between male Spotted Owls and female Barred Owls (Haig et al. 2004). This makes sense when considering that male owls often present females with food during courtship: male Barred Owls presenting non-mammalian prey to female Spotted Owls would not result in a successful courtship.

### **Parasites**

As a recent but closely-related invader to the west coast, Barred Owls have the potential to bring novel, harmful pathogens and parasites from east coast populations which could be transmitted to Spotted Owls. As such, Lewicki et al. (2015) examined the *Haemoproteus* blood parasite assemblages of Barred Owls in both their native and invasive ranges and Northern Spotted Owls. They found that Northern Spotted Owls had a slightly lower prevalence of *Haemoproteus* infection than both populations of Barred Owls, but

mean infection intensity was almost 100 times greater than that of western Barred Owls. They noted their results suggested that *Haemoproteus* in Spotted Owls are not solely influenced by Barred Owls. They did not directly evaluate if and to what extent parasite infection may have influenced fitness but noted that parasites can become pathogenic with additional stressors, such as competition with Barred Owls.

### **The future of Spotted Owl and Barred Owl populations**

Gutiérrez et al. (2004) outlined and discussed the uncertainty of the ultimate outcome of the invasion of the Barred Owl on the future of these two species. They listed nine potential futures for the Northern Spotted Owl, listed in order of their outcome from most serious to least serious effect:

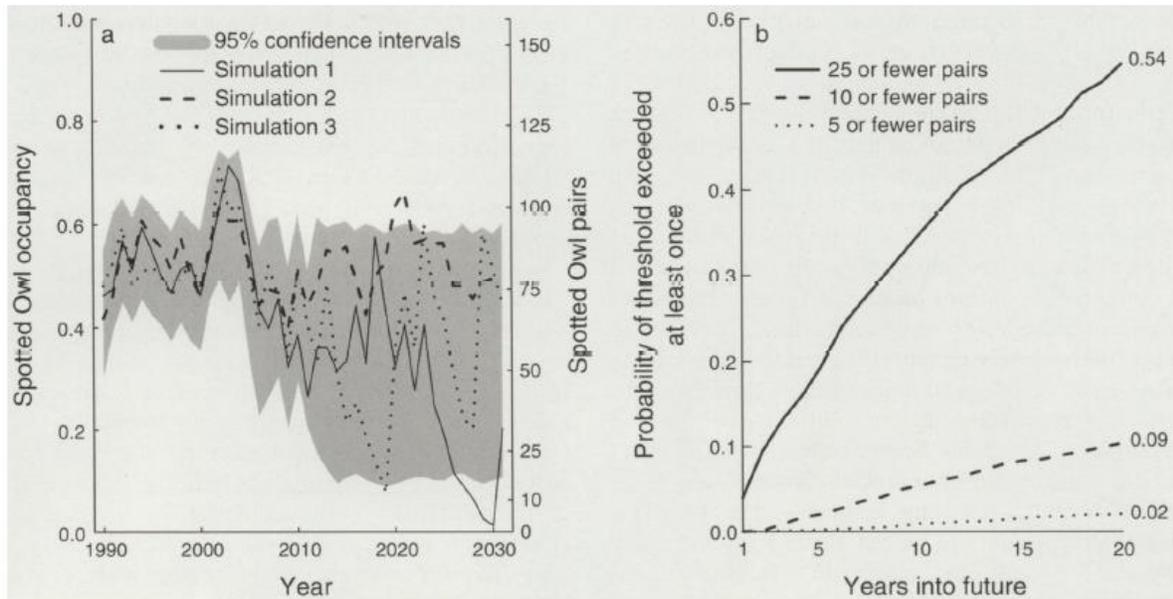
1. Barred Owls will replace the Northern Spotted Owl throughout its range (behavioral and competitive dominance hypothesis).
2. Barred Owls will replace the Northern Spotted Owl in the northern, more mesic areas of its range (moisture-dependent hypothesis).
3. Barred Owls will replace Northern Spotted Owls over much of its range, but the Spotted Owl could persist in some areas with management intervention (management hypothesis).
4. Barred Owls will replace Northern Spotted Owls over much of its range, but the Spotted Owl will persist in refugia (refugia hypothesis).
5. Barred Owls will replace Northern Spotted Owls in the northern part of its range but the Spotted Owl will maintain a competitive advantage in habitats where its prey is abundant and diverse (specialist vs. generalist hypothesis).
6. Barred Owls will replace Spotted Owls only where weather and habitat change have placed Spotted Owls at a competitive disadvantage (synergistic effects hypothesis).
7. Barred Owls will replace Northern Spotted Owls in some habitats but not in others (habitat hypothesis based on structural elements of forest, which confer a maneuverability advantage to the smaller Spotted Owl).
8. Barred Owls and Spotted Owls will compete, with the outcome being an equilibrium favoring Barred Owls over Spotted Owls in most but not all of the present Northern Spotted Owl habitat range (interference competition hypothesis).
9. Barred Owls will increase to a peak number, then decline or stabilize at a lower density, which will permit the continuation of Spotted Owls (dynamics hypothesis).

As noted earlier, the presence of Barred Owls has led to an increase in Northern Spotted Owl extinction rates (Dugger et al. 2011, 2016; Kroll et al. 2010; Olson et al. 2005; Sovern et al. 2014, Yackulic et al. 2014). Sovern et al. (2014) stated that the positive relationship between Barred Owl detections and extinction probabilities suggests that Spotted Owls are being displaced because of competition with Barred Owls. Modelling of future populations by Yackulic (2017) found that, without management interventions, the Northern Spotted Owl will be extirpated from most or all of its geographic range; however this may take anywhere from decades to millennia.

Two-species model simulations of the Tyee, Oregon, study area suggest that Spotted Owl numbers will be depressed, but not completely excluded from the study area by 2030 (**Fig. 8a**; Yackulic et al. 2014). However, the authors note that, in some simulation runs, the Spotted Owl population fell to  $\leq 25$  pairs,

where small-population effects might become important (**Fig. 8b**). Further, simulation runs assumed an outside source of Spotted Owls for colonization, which at some point may not be available.

In addition to direct competition between Spotted and Barred owls, the addition of the Barred Owl as a similar, but novel and invasive, predator to these ecosystems can greatly impact the food web and associated ecological processes, affecting the ability of the ecosystem to support the populations of two similar predators (Holm et al. 2016). Holm and his colleagues explored the potential effects of adding Barred Owls to the ecosystem on the food web, including restructuring of prey communities, changes in prey behavior, increased predation pressure for shared primary prey species (such as northern flying squirrels, red tree voles, and lagomorphs), and declines in secondary prey species.

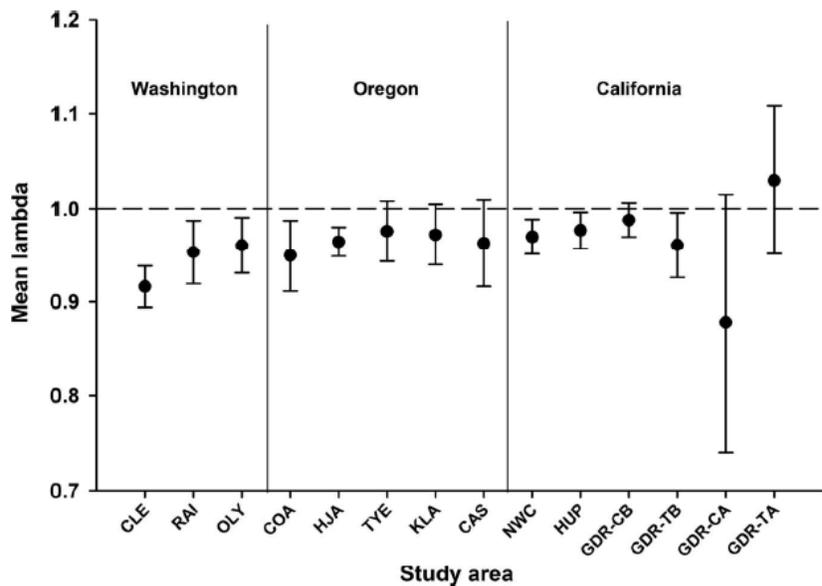


**Figure 8.** Northern Spotted Owl occupancy estimated over the course of the 22-year study and simulated over the next 20 years. (a) The fitted model predicts coexistence; however, this prediction assumes that colonization rates are unrelated to conspecific occupancy levels within the study region (i.e., the prediction assumes there that there is an outside source of colonists). (b) Simulations suggest that there is a high probability that the population will dip below certain thresholds where small-population effects might be important. For example, in 54% of the simulations, the population fell below 25 pairs at least once over 20 years, in 9% of simulations, the population fell below 10 pairs, and in 2.4% of simulations, the population fell below five pairs within 20 years. From Yackulic et al. (2014).

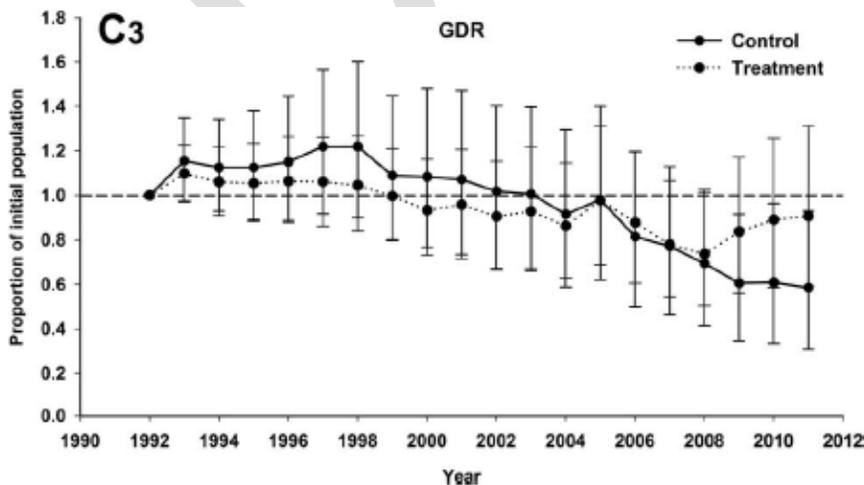
## Management actions

A two-day workshop in 2005 was convened to discuss approaches to combat the threat of the Barred Owl invasion to Northern Spotted Owls (Buchanan et al. 2007). Suggestions ranged from no action, to removing Barred Owls using lethal methods. The final recommendation was that emphasis should be on removal experiments and on intensive field studies on aspects of Barred Owl life history and interspecific interactions. Removal of Barred Owls has also been suggested by others (Courtney and Franklin 2004, Gutiérrez et al. 2007), noting that it would have the added benefit of ascertaining the effect of Barred Owls on Spotted Owls.

Diller et al. (2014) began removing Barred Owls on Green Diamond Resources lands in northern California in 2009 as a pilot study to develop methods and study design and to evaluate the feasibility of a removal program. They determined that it was a relatively quick, effective, and low-cost program. Following removal, Spotted Owl occupancy made a slow recovery in areas where Barred Owls were removed compared to untreated areas where occupancy declined, while Barred Owl occupancy declined (Diller et al. 2016). Spotted Owl fecundity rates did not change in the treated areas, however the greater number of pairs in treated areas resulted in greater overall population productivity; there was also an increase in estimated survival and population change, and a decrease in extinction rate. Barred Owl removals continued through 2013, resulting in an increased rate of population change (Fig. 9) as well as realized increased population change (Fig. 10) (Dugger et al. 2016). In 2015, Wiens et al. (2017) began a 5-year Barred Owl removal study in established study areas in Washington and Oregon. After removal, they noted a decline in the probability of use by territorial pairs of Barred Owls on both the control and treatment areas between 2015 and 2016, which they felt might indicate a decline not directly attributable to experimental removal activities.



**Figure 9.** Estimated mean rates of population change and 95% confidence intervals for Northern Spotted Owls from the random effects intercept-only model in each of 11 study areas in Washington, Oregon, and California, USA, 1985–2013. Estimates for the GDR study area are presented separately for control and treatment areas before (1990–2008) and after (2009–2013) Barred Owls were removed. See Appendix A for study area abbreviations. From Dugger et al. (2016).

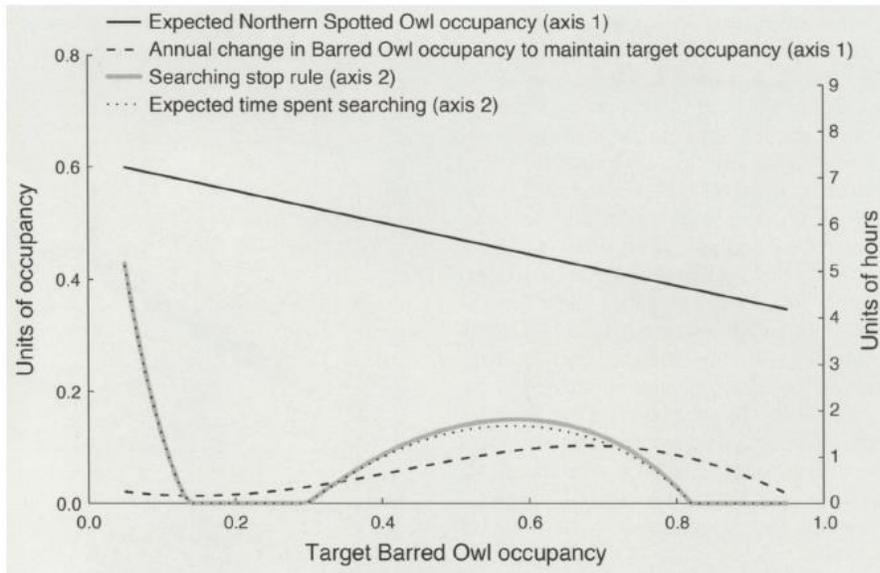


**Figure 10.** Annual estimates of realized population change ( $D_t$ ) with 95% confidence intervals for Northern Spotted Owls at Green Diamond Resources in California, USA. Estimates for the GDR study area are presented separately for control and treatment areas in relation to Barred Owl removals beginning in 2009. Graphs A-C2 for additional study areas are not presented here. From Dugger et al. (2016).

The question remains if such an approach would be successful and feasible throughout the Northern Spotted Owl range. Bodine and Capaldi (2017) used mathematical modelling to determine if removing Barred Owls could ultimately save the Northern Spotted Owl population in the Oregon Coast Range. Their models showed that Barred and Northern Spotted owls could not coexist in the long run, suggesting that Barred Owls would need to be eliminated. They determined that, without any action, by 2030 less than 5% of historical Spotted Owl sites would contain Spotted Owls. However, elimination of Barred Owls would require clearing about 50% of the Barred Owl sites per year to remove them in over 100 years. To eliminate them in 10 years, it would take removing over 90% of Barred Owl sites yearly. However, their analyses do not include Barred Owl immigration to the region. Perlman (2017) examined the effects of various Barred Owl removal rates in four existing demographic Northern Spotted Owl study areas using a two-species individual-based model. She found that viable, long-term recovery was observed for only two of the four areas, and was dependent on high removal intensities. No model showed a return to pre-invasion population numbers. However, her models agree with Bodine and Capaldi, in that with no removal action taken, the Northern Spotted Owl population would go extinct within 100 years. Baumbusch (2016) investigated the effect of size of patch on removals with modelling and found that large contiguous removal areas maintained a lower Barred Owl occupancy and required removal of fewer owls compared to small fragmented removal areas covering the same acreage.

By contrast, Yackulic et al. (2014) noted that complete eradication of Barred Owls is unlikely, but that it might be more feasible to maintain their occupancy at a low level (0.2), benefitting Spotted Owls while decreasing cost (**Fig. 11**). They suggested that initial removal effort be focused on patches with high quality habitat, where Spotted Owls have typically had high reproductive rates or are currently or have recently been observed to be occupied by Spotted Owls. Holm et al. (2016) suggested that removal efforts would be most effective in areas with low Barred Owl populations and where it would be defensible against Barred Owl colonization or have high-quality Spotted Owl habitat. Yackulic et al. (2012) noted that understanding the influence of regional occupancy on local colonization and extinction rates of Barred Owls will be important to predict the impacts of Barred Owl removal as a management tool.

Diller et al. (2014) found the cost for such removals not to be overly burdensome, costing up to \$150/owl in direct costs. On the other hand, Livezey (2010) estimated cost to be about \$1 million annually for the entire Northern Spotted Owl range, including additional indirect costs, breaking down to about \$700/owl in the first year and \$2800/owl in subsequent years. Ultimately, there are also questions about interfering with a natural process of competition and how long any removal program could last, since there would still likely be immigration from the east, if not from the much closer Barred Owl populations in Canada to the north (Bodine and Capaldi 2017, Cornwall 2014). Public acceptance of such methods may also be difficult to overcome (Lute and Attari 2017). Other authors noted that habitat management may aid the Spotted Owl or that a natural balance between Barred and Spotted Owls has or can be achieved at least in certain areas, allowing for coexistence between the species (Buchanan et al. 2007, Pearson and Livezey 2007).



**Figure 11.** Comparison of the expected costs and benefits of hypothetical management of Barred Owl occupancy suggests that maintaining Barred Owls at relatively low occupancies (~0.2) may minimize long-term costs, while also benefiting Northern Spotted Owls nearly as much as eradication would benefit them. The benefit is expressed as the expected average occupancy of Northern Spotted Owls. Costs can be measured either in terms of the number of Barred Owls that would have to be removed annually to maintain a given level of Barred Owl occupancy or as the expected number of hours surveyors would have to spend searching at each site to ensure the appropriate number of removals.

### Important information gaps

1. Effects of disturbance on Barred Owls. The influence of fuel treatments and thinning on Spotted Owl occupancy has been repeatedly explored. Determining how variation in such treatments affects Barred Owl colonization, and their subsequent effects on Spotted Owls, represents an important line of inquiry.
2. Interactive effects of Barred Owls and fire on Spotted Owls. Barred Owls can use a wider range of habitats and food resources than Spotted Owls. Such behavioral flexibility may make Barred Owls relatively more successful in burned landscapes than Spotted Owls. To our knowledge this conjecture remains unverified.
3. Recolonization rates of Barred Owls after their removal. The positive response of Spotted Owls to Barred Owl removal has been encouraging. However, the rate at which Barred Owl recovery occurs post-removal is unknown and would greatly inform planning for future removal efforts.
4. Influence of Barred Owls on California Spotted Owls. The expansion of Barred Owls into the Sierra Nevada raises several pressing questions. Will the Barred Owl exert less, more, or the same negative influence on California Spotted Owl populations?

### **Key Messages for Managers**

- Barred Owls reduce Spotted Owl occupancy, survival, productivity, fecundity, and population growth.
- Barred Owls exhibit a wide dietary breadth and are likely influencing food webs in unforeseen ways.
- Be cautious in assuming that recently arrived Barred Owls will remain in low numbers in perpetuity. Barred Owls have repeatedly shown that they occur in low numbers prior to dramatically increasing in abundance.
- Barred Owls appear to suppress detection probabilities of Spotted Owls. Consider alternative techniques, such as scat sniffing dogs, or increasing survey effort to detect Spotted Owls.
- Experimental removal of Barred Owls has proven effective in improving Spotted Owl population growth.
- Maximize the value of Barred Owl removals by focusing on those habitats most valuable for Spotted Owls with the least number of Barred Owls, prior to removals in poor habitat with high numbers of Barred Owls.

### **Annotated Bibliography of Cited References**

Anthony, R.G., E.D. Forsman, A.B. Franklin, D.R. Anderson, K.P. Burnham, G.C. White, C.J. Schwarz, J. Nichols, J.E. Hines, G.S. Olson, S.H. Ackers, S. Andrews, B.L. Biswell, P.C. Carlson, L.V. Diller, K.M. Dugger, K.E. Fehring, T.L. Fleming, R.P. Gerhardt, S.A. Gremel, R.J. Gutiérrez, P.J. Happe, D.R. Herter, J.M. Higley, R.B. Horn, L.L. Irwin, P.J. Loschl, J.A. Reid, and S.G. Sovern. 2006. Status and trends in demography of Northern Spotted Owls, 1985–2003. *Wildlife Monographs* 163:1-48.

As part of a meta-analysis of the demography of the Northern Spotted Owl across its range, the authors included the effect of Barred Owls on demographic parameters such as recapture probabilities, apparent survival, and fecundity. They hypothesized that the overall apparent lack of effect on fecundity or survival that they found was due to Barred Owls potentially having a greater effect on Spotted Owl occupancy of territories.

Bailey, L.L. J.A. Reid, E.D. Forsman, and J.D. Nichols. 2009. Modeling co-occurrence of Northern Spotted and Barred owls: Accounting for detection probability differences. *Biological Conservation* 142(12):2983-2989.

Authors investigated the co-occurrence of Northern Spotted and Barred owls using detection probabilities and spatial patterns with a two-species model. They found no evidence that Barred Owls excluded Spotted Owls from territories or that the two species co-occurred less often than expected. Detection probabilities for the two species were substantially different, with the Spotted Owls having a higher detection probabilities for both day and night surveys. Detection probabilities were mostly independent; however daytime surveys were less so – that is, that if you detected one species, you were unlikely to detect the other species.

Baumbusch, R.C. 2016. A model to evaluate Barred Owl removal strategies for the conservation of Northern Spotted Owls. M.S. Thesis, Humboldt State University, Arcata, CA. 68 p.

Using individual-based modelling, the author compared alternative spatial strategies for removing Barred Owls in a localized area. Using an array of patches of identical size, he compared the effectiveness of large, continuous areas to several designs of progressively smaller, fragmented areas with different distribution. Effectiveness was evaluated using occupancy rates within the removal areas, while efficiency was measured by the number of owls removed annually. Larger, continuous removal areas maintained lower Barred Owl occupancy rates than smaller, fragmented ones, and while the number of owls removed was greater, the number of owls removed per patch per year was lower than for other patch arrays.

Bodine, E.N. 2017. Can culling Barred Owls save a declining Northern Spotted Owl population? *Natural Resources Modelling* 30(3). DOI: 10.1111/nrm.12131.

The authors modelled competition between Spotted and Barred owls of the Oregon Coast region using information theory. Their analysis shows that even with culling Barred Owls, no model contained a coexistence equilibrium given the current growth and competition parameters. Therefore, the authors conclude, complete elimination of the Barred Owl population is required for conservation of the Spotted Owl population, with a culling rate around 90% of the sites per year to eliminate the Barred Owl population within 10 years. However, they noted their analysis does not take into account the continual influx of Barred Owls from the east coast.

Buchanan, J.B., T.L. Fleming, and L.I. Irwin. 2004. A comparison of Barred Owl and Spotted Owl nest-site characteristics in the eastern Cascade Mountains, Washington. *Journal of Raptor Research* 38:231–237.

Ten Barred Owls nests found in the course of timber-sale evaluations in the eastern Cascade mountains from 1988-1994 are described, including the nest, nest tree, and surrounding vegetation. These were compared with a sample of Spotted Owl nests from a previous investigation. Among the findings were that Barred Owl nests were generally in areas with low relief, while Spotted Owls nested on significantly steeper terrain. Elevation of Barred Owl nest locations was not significantly different from Spotted Owl nests. There was little difference in the vegetation surrounding the nest trees.

Buchanan, J.B., R.J. Gutiérrez, R.G. Anthony, T. Cullinan, L.V. Diller, E.D. Forsman, and A.B. Franklin. 2007. A synopsis of suggested approaches to address potential competitive interactions between Barred Owls (*Strix varia*) and Spotted Owls (*S. occidentalis*). *Biological Invasions* 9:679–691.

The authors present a synthesis of ideas developed and expressed at a workshop to consider how to manage the potential threat of Barred Owls to the viability of the Spotted Owl, and summarizes the suggested management actions and potential studies to address key management questions. Suggestions include no action, more studies, removal experiments of

immature Spotted Owls, culling Barred Owls, habitat management, supplemental feeding, and disrupting Barred Owl reproduction.

Courtney, S. and A. Franklin. 2004. Chapter twelve: Information needs. Pages 12-1–12-18 in S. Courtney, ed. Scientific evaluation of the status of the Northern Spotted Owl. Sustainable Ecosystems Institute, Portland, OR.

As part of the five-year status review report on the Northern Spotted Owl, past and present information needs for management of the Northern Spotted Owl are reviewed, including information needs on competition with Barred Owls. These include basic natural history of Barred Owls in the Pacific Northwest, development of an appropriate Barred Owl covariate, Barred Owl use of lands set aside in the Northwest Forest Plan for Northern Spotted Owls, and understanding the magnitude and mechanisms of competition between the two species.

Crozier, M.L., M.E. Seamans, R.J. Gutiérrez, P.J. Loschl, R.B. Horn, S.G. Sovern, and E.D. Forsman. 2006. Does the presence of Barred Owls suppress the calling behavior of Spotted Owls? *Condor* 18:760-769.

The authors examined whether the response frequency of naive and experienced Spotted Owls to simulated Spotted Owl calls differed after exposure to simulated Barred Owl calls. Summarizing an experiment using taped Spotted and Barred Owl calls, they found that both subspecies of Spotted Owl responded less to Spotted Owl calls after exposure to Barred Owl calls and Northern Spotted Owls responded less frequently in areas having higher numbers of Barred Owls. They inferred that the simulated presence of a Barred Owl might negatively affect Spotted Owl response.

Dark, S.J., R.J. Gutiérrez, G.I. Gould, Jr. 1998. The Barred Owl (*Strix varia*) invasion in California. *Auk* 115:50–56.

Review of sightings of Barred Owls in California from 1981 to 1996. Sightings, or “sites”, were placed into three time periods corresponding to (1) the establishment of statewide surveys by the U.S. Forest Service, (2) beginning of demographic studies in northwestern California and the Sierra Nevada, and (3) start of intensive surveys for Spotted Owls mandated by the federal government. The authors noted that Barred Owl territories were significantly lower in elevation than Spotted Owl territories, both for the authors’ studies at Redwood National Park and analysis of observations from the California Department of Fish and Game regional database. Two Northern Spotted Owl pairs were displaced by Barred Owl pairs in their study area.

Davis, R.J., B. Allen, J. Hollen, J.E. Gower and D. Keenum. 2016. Status and trends of Northern Spotted Owl habitats. Gen. Tech. Rpt. PNW-GTR-929. USDA Forest Service, Pacific Northwest Research Station, Portland, OR. 54 p.

The authors analyzed the effect of Barred Owls on Northern Spotted Owl habitat selection in the course of evaluating habitat status trends for the Northern Spotted Owls. They found a strong negative correlation between the increasing trend of Spotted Owl territories with Barred Owl detections and average Habitat Suitability at Spotted Owl locations in the Tyee, Oregon, study area. Over 23 years, Habitat Suitability was significantly lower if there were Barred Owls detected, suggesting that Spotted Owls were choosing habitat of a lower quality.

Diller, L.V., J.P. Dumbacher, R.P. Bosch, R.R. Brown, and R.J. Gutiérrez. 2014. Removing Barred Owls from local areas: Techniques and feasibility. *Wildlife Society Bulletin* 38:211–216.

Reviews the results of the first Barred Owl removal study, in which the feasibility and cost of removing Barred Owls using lethal methods within the context of a removal experiment in northern California was examined. The authors determined that lethal removal of Barred Owls was rapid, technically feasible, and cost-effective. They review the ease of locating and identifying Barred Owls and noted that new, colonizing Barred Owls replaced those that were removed.

Diller, L.V., K.A. Hamm, D.A. Early, D.W. Lamphear, K.M. Dugger, C.B. Yackulic, C.J. Schwarz, P.C. Carlson, and T.L. McDonald. 2016. Demographic response of Northern Spotted Owls to Barred Owl removal. *Journal of Wildlife Management* 80(4):691–707. DOI: 10.1002/jwmg.1046.

Summary of the results of a Barred Owl 2009-2010 culling experiment in northern California. The treated areas did not result in an increased Spotted Owl fecundity, but did result in a decrease in Spotted Owl extinction rates to one similar to areas without Barred Owls, leading to an increase in apparent survival and annual rate of population change.

Dugger, K.M., R.G. Anthony, and L.S. Andrews. 2011. Transient dynamics of invasive competition: Barred Owls, Spotted Owls, habitat, and the demons of competition present. *Ecological Applications* 21(7):2459–2468.

The authors used the recent expansion of Barred Owls into the range of the endemic Northern Spotted Owl to directly explore competition processes using single-species, multi-season occupancy models, quantifying Barred Owl detections and habitat characteristics to model extinction and colonization rates of Spotted Owl pairs in southern Oregon. There was strong support for an association between detection of Barred Owls and increased extinction and decreased colonization rates of Spotted Owl pairs. The analyses provided evidence of interference competition between the species. Presence of Barred Owls resulted in lower occupancy rates where they were detected, lower colonization rates, and higher extinction rates.

Dugger, K.M., E.D. Forsman, A.B. Franklin, R.J. Davis, G.C. White, C.J. Schwarz, K.P. Burnham, J.D. Nichols, J.E. Hines, C.B. Yackulic, P.F. Doherty, Jr., L. Bailey, D.A. Clark, S.H. Ackers, L.S. Andrews, B. Augustine, B.L. Biswell, J. Blakesley, P.C. Carlson, M.J. Clement, L.V. Diller, E.M. Glenn, A. Green, S.A. Gremel, D.R. Herter, J.M. Higley, J. Hobson, R.B. Horn, K.P. Huyvaert, C.

McCafferty, T. McDonald, K. McDonnell, G.S. Olson, J.A. Reid, J. Rockweit, V. Ruiz, J. Saenz, and S.G. Sovern. 2016. The effects of habitat, climate, and Barred Owls on long-term demography of Northern Spotted Owls. *Condor* 118:57–116.

The authors evaluated population processes of the Northern Spotted Owl in 11 study areas in Washington, Oregon, and northern California from 1985-2013, including competition with Barred Owls. They found that Barred Owl presence was associated with increased local extinction rates of Spotted Owl pairs and had a negative effect on apparent survival of Spotted Owls most study areas. They suggested that Barred Owl densities may now be high enough across the range of the Northern Spotted Owl that, despite the continued management and conservation of suitable owl habitat on federal lands, the long-term prognosis for the persistence of Northern Spotted Owls may be in question without additional management intervention.

Funk, W.C., T.D. Mullins, E.D. Forsman, and S.M. Haig. 2007. Microsatellite loci for distinguishing Spotted Owls (*Strix occidentalis*), Barred Owls (*Strix varia*), and their hybrids. *Mol. Ecol. Notes* 7: 284–286.

The authors identified four microsatellite loci that correctly distinguishes between Spotted Owls, Barred Owls, F<sub>1</sub> hybrids, and backcrosses. They tested 90 owls that were initially identified in the field using plumage characteristics. Those specimens field identified to species were confirmed as correctly identified using these loci. Four owls confidently identified as F<sub>1</sub> hybrids were also correctly identified. However, of eight field-identified as potential F<sub>1</sub> hybrids and backcrosses, five (more than half) were misidentified in the field and were either Spotted or Barred owls, not hybrids.

Glenn, E.M., R.G. Anthony, and E.D. Forsman. 2010. Population trends in Northern Spotted Owls: Associations with climate in the Pacific Northwest. *Biological Conservation* 143:2543-2552.

In the course of modeling population trends with climate for Northern Spotted Owl, the authors found that declines in recruitment at four of six sites were also associated with increased presence of Barred Owls. At two sites, they also found annual survival was negatively associated with the proportion of Spotted Owl territories containing Barred Owl detections. Only at one site did the presence of Barred Owls have a negative effect of numbers of young fledged per year.

Glenn, E.M., R.G. Anthony, E.D. Forsman, and G.S. Olson. 2011a. Local weather, regional climate, and annual survival of the Northern Spotted Owl. *Condor* 113:159–176.

Survival was negatively associated with Barred Owls at one area but not in five other areas. In a regional meta-analysis, the authors found that Barred Owls accounted for only slight amounts of temporal variation in survival. However, the parameter estimates indicated that Barred Owls were negatively associated with survival at all six areas.

Glenn, E.M., R.G. Anthony, E.D. Forsman, and G.S. Olson. 2011b. Reproduction of Northern Spotted Owls: The role of local weather and regional climate. *Journal of Wildlife Management* 75:1279-1294.

The authors analyzed the relationships between reproduction and several climate variables at varied spatial and temporal scales. Though Barred Owl influence on reproduction was not the primary focus, they also included the presence of the species in some analyses. They observed a negative association between reproduction and the presence of Barred Owls only at one of four sites; however in a meta-analysis there was a negative association at most sites.

Graham, Scott A. 2012. Diet composition, niche and geographic characteristics, and prey size preference of Barred Owls (*Strix varia*) in the Pacific Northwest. M.S. Thesis, Boise State University, Boise, ID. 149 p.

The author describes the dietary composition, niche, geographic characteristics, and prey size preference of the Barred Owl in the Pacific Northwest. His primary study site was in Western Oregon in 2007-2009. He analyzed regurgitated pellets and found their diets comprised 64.8% mammals, followed by birds, reptiles, amphibians, and others. Diets were generally dominated by northern flying squirrels (*Glaucomys sabrinus*). Barred Owls had a high taxonomic richness in its diet, indicating the versatility and range of prey they consumed. He expanded his study to other study sites in Oregon and Northwest Washington and found diets varied between sites, with the central Coast Ranges and Olympic National park having similar diets, dominated by forest mammals, and the eastern Cascades had diets where insects were the most numerous taxa. In controlled lab experiments, both Northern Spotted Owls and Barred Owls preferred smaller mice over larger rats.

Gutiérrez, R.J., M. Cody, S. Courtney, A.B. Franklin. 2007. The invasion of Barred Owls and its potential effect on the Spotted Owl: A conservation conundrum. *Biological Invasions* 9:181-196. DOI 10.1007/s10530-006-9025-5.

The authors evaluated the potential negative impact of Barred Owls on Spotted Owls by reviewing relevant literature of studies of sympatric owls, from which they concluded that there should be strong competition between the two species making a stable coexistence unlikely. They also reviewed results of recent Spotted Owl studies that included Barred Owls, noting that because Barred Owls have similar sizes of broods, smaller territories, and share similar habitat preferences, then they will have some degree of competition. This could be ameliorated if the Spotted Owl occupies habitat outside of the preferred habitat of Barred Owls. They also noted that these species have similar dietary preferences, though the Barred Owl is a food generalist, so by competing for the same prey the prey population that is shared between the two species could be sufficiently reduced such that the Spotted Owl may not be able to find sufficient food.

Gutiérrez, R.J., M. Cody, S. Courtney, and D. Kennedy. 2004. Chapter seven: Assessment of the potential threat of the Northern Barred Owl. Pages 7-1 to 7-51 in: Courtney, S.P., J.A. Blakesley, R.E. Bigley, M.L. Cody, J.P. Dumbacher, R.C. Fleischer, A.B. Franklin, J.F. Franklin, R.J. Gutiérrez, J.M.

Marzluff, and L. Sztukowski. Scientific evaluation of the status of the Northern Spotted Owl. Sustainable Ecosystems Institute, Portland, OR. 507 p.

As part of the five-year review for the Northern Spotted Owl, the authors review current information about the Barred Owl, noting that most data on the Barred Owl in the Pacific Northwest was recorded incidental to Northern Spotted Owl surveys. The authors also discuss the differences and similarities between the two species in body size, habitat use, and prey, and compare the current situation to that of *Strix* owls coexisting sympatrically in other areas. They note that two subspecies of the Spotted and Barred owls already coexist in northern Mexico: Mexican Spotted Owl [*S. o. lucida*] and Mexican Barred Owl [*S. v. sartorii*]. The Mexican Barred Owl is estimated at twice the mass as the Mexican Spotted Owl allowing for coexistence. However, the Northern Spotted Owl and Northern Barred Owl are much more similar in mass. They outline nine possible hypotheses regarding the potential consequences of the Barred Owl invading the range of the Northern Spotted Owl.

Gutiérrez, R.J., A.B. Franklin and W.S. Lahaye. 1995. Spotted Owl (*Strix occidentalis*), The Birds of North America (P.G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: <https://birdsna.org/Species-Account/bna/species/spowl>. DOI: 10.2173/bna.179. Last accessed 7/30/2018.

The authors describe the Spotted Owl's appearance, systematics, distribution, habitat, general biology, behavior, subspecies, conservation and management. Spotted Owls are associated with late seral stage conifer forests in the western North America and Mexico. The Northern Spotted Owl forages almost exclusively on small and medium-sized mammals, the other two subspecies also include a fair amount of birds and invertebrates. They forage primarily at night. They lay one clutch per breeding season of 1 to 4 eggs using existing structures such as cavities, broken-top trees, and abandoned nests.

Haig, S.M., T.D. Mullins, E.D. Forsman, P.W. Trail, and L. Wennerberg. 2004. Genetic identification of Spotted Owls, Barred Owls, and their hybrids: Legal implications of hybrid identity. *Conservation Biology* 18(5):1347-1357.

The authors used mitochondrial gene analysis to distinguish between Northern Spotted Owls and Barred Owls, and found them to be in two distinct clades with no signs of previous introgression, as well as extensive divergence between the two species. Hybrids had unique genetic combinations and were most frequently due to crosses between female Barred Owls and male Spotted Owls.

Hamer, T.E., D.L. Hays, C.M. Senger, and E.D. Forsman. 2001. Diets of Northern Barred Owls and Northern Spotted Owls in an area of sympatry. *Journal of Raptor Research* 35:221–227.

The authors collected regurgitated pellets from Spotted and Barred owl territories in Washington state from 1985-1989 during the spring and summer. They found Spotted Owl diet consisted almost entirely of mammals (98.6% biomass), while Barred Owls were more general

(74.5% mammal biomass). There was a 76% overlap in diets. The most important prey in diets of Spotted Owls and Barred Owls were northern flying squirrels (*Glaucomyssa brinus*) and snowshoe hares, respectively. Barred Owls ate more diurnal species and terrestrial species, while Spotted Owls ate more arboreal species. Overall, Barred Owls had a more diverse diet than Spotted Owls.

Hamer, T.E., E.D. Forsman, A.D. Fuchs, and M.L. Walters. 1994. Hybridization between Barred and Spotted owls. *Auk* 111:487–492.

The authors list and describe 3 adult and 1 yearling hybrids found in Oregon and Washington from 1989-1991. All were identified by unique plumage characteristics, vocalizations, and measurements. The body mass of all adults was as great as or greater than average values for the Barred Owl and greater than the upper limits for Spotted Owls. However, the wing chord and tail lengths were intermediate between the two parent species. They also describe the differences in the calls compared to the two species.

Hamer, T.E., E.D. Forsman, and E.M. Glenn. 2007. Home range attributes and habitat selection of Barred Owls and Spotted Owls in an area of sympatry. *Condor* 109:750–768.

Researchers radio-tagged Spotted and Barred Owls in the northern Cascades Range in Washington state. Spotted Owls had home ranges about 2-5 times larger than those of Barred Owls. The greatest differences were shown by females, with a home range averaging 6.7 times larger than female Barred Owls. Barred Owl winter home ranges were larger and tended to be expansions of the summer range, similar to some Spotted Owls. Both species used old forest habitat, though this was more significant for Spotted Owls. Spotted Owls were found at higher elevations on average than Barred Owls and selected areas near perennial streams in contrast to Barred Owls who showed no preference.

Hanna, Z.R., J.P. Dumbacker, R.C.K. Bowie, J.B. Henderson, and J.D. Wall. 2018. Whole-genome analysis of introgression between the spotted owl and barred owl (*Strix occidentalis* and *Strix varia*, respectively; Aves: Strigidae) in western North America. bioRxiv, doi: <http://dx.doi.org/10.1101/343202>. Last accessed 7/30/2018.

The authors examined genome sequence data from 51 Barred and Spotted owls to investigate introgression between the species. They did confirm genetically that these species do hybridize and backcross, but found no evidence of widespread introgression which could lead to genetic swamping of the Spotted Owl and erase their genome. All non-hybrid individuals were either pure Spotted Owls or pure Barred Owls. They also found no significant difference in ancestry between the eastern and western Barred Owls they tested.

Herter, D.R. and L.L. Hicks. 2000. Barred Owl and Spotted Owl populations and habitat in the central Cascade Range of Washington. *Journal of Raptor Research* 34:279–286.

The authors surveyed for Spotted and Barred owls in western Washington using taped calls and vocal imitations from 1991-1993. They found Barred Owls at greatest densities on the wetter, western portions of the Cascade Range. On the drier, eastern portions of the range, Barred Owls were usually found along major river and stream corridors, in the vicinity of forested wetlands, or at higher elevations receiving increased precipitation. Spotted Owls used sites with greater amounts of mature coniferous forest than did Barred Owls within 0.8 km of site centers. They found no evidence of mixed-species pairing or hybrids.

Hollenbeck, J.P., S.M. Haig, E.D. Forsman, and J.D. Wiens. 2018. Geographic variation in natal dispersal of Northern Spotted Owls over 28 years. *Condor* 120: 230-542. DOI: 10.1650/CONDOR-17-164.1.

Net natal dispersal distances varied by four ecoregions, but declined similarly over time (~1 km/yr). Dispersal direction also varied by ecoregion: bimodal (north-south) in the Oregon Coast Range, south-southwest in the Oregon and California Cascades, and little directionality in the remaining regions. Distances also varied by ecoregion (mean 62.3-99.5 km), with the longest dispersals (up to 177 km) originating in the southern-most ecoregions. There was no direct relationship between Barred Owl detections near natal or settling locations and dispersal distance.

Holm, S.R., B.R. Noon, J.D. Wiens, and W.J. Ripple. 2016. Potential trophic cascades triggered by the Barred Owl range expansion. *Wildlife Society Bulletin* 40(4):615-624.

The authors identify possible direct and indirect ecological consequences following invasion of the Barred Owl into forest ecosystems of the west coast. They reviewed and evaluated current information on potential widespread ecological changes triggered by an increase in abundance of the Barred Owl as a new nocturnal avian predator, focusing on potential behavioral and adaptive changes in prey populations. They explored how Barred Owls at high density may affect ecosystem functions via indirect changes to food-web dynamics and predator-prey relationships. They discussed how this could lead to niche displacement or competitive exclusion of the Spotted Owl by the Barred Owl. They hypothesized that expanding Barred Owl populations will result in increased predation pressure on traditional and naïve prey species within the range of the Northern Spotted Owl. Initially, the largest declines would be in the prey species utilized by both owl species, such as the northern flying squirrel, red tree vole, and lagomorphs. In turn, this could lead to potential declines in sensitive species, effects on the predator communities, and indirect effects on ecosystem processes.

Irwin, L.L., D.F. Rock, and S.C. Rock. 2017. Barred owl habitat selection in west coast forests. *Journal of Wildlife Management* 82(1):202–216.

Barred Owls were radio-tagged at Chehalis, Washington, Springfield, Oregon, and Arcata, California. Data suggested that Barred Owls selectively hunted in lower-slope positions on southern aspects, often near streams at low elevations near nests. They also appeared to avoid clearcuts and young plantations. At Arcata, high densities of Douglas-fir (*Pseudotsuga*

*menziesii*) trees and increasing basal area of tanoak (*Notholithocarpus densiflorus*) were negatively associated with barred owl habitat selection.

Iverson, Wayne F. 2004. Reproductive success of Spotted Owls sympatric with Barred Owls in western Washington. *Journal of Raptor Research* 38(1):88-91.

The author compared reproductive success for Spotted Owls nesting in western Washington for sites with Barred Owls within 0.8 km of the nest, within 2.5 km, and not within 2.5 km. He found no significant difference in reproductive success (percent fledged) between these three groups. Nor was there significant difference in mean amount of older forest available or the mean elevation of these sites. The author speculated that the success of Spotted Owls despite the presence of Barred Owls may be due to differences in their diets on the west slopes of the Cascades, as described by other researchers.

Jennings, S., R.L. Cormier, T.G. Gardali, D.T. Press, and W.W. Merkle. 2011. Status and distribution of the Barred Owl in Marin County, California. *Western Birds* 42:103–110.

The authors summarize and discuss detections of Barred Owls in Marin County, California, at the furthest southern extent of the Barred Owl's current coastal range, gathering citizen science data and other incidental data to augment data from the Northern Spotted Owl monitoring programs by federal and county authorities from 2002-2010. The first Barred Owl was detected in 2002. Since then, 107 detections of Barred Owls have been recorded. Barred Owls successfully raised young in 2007 and 2008 in Muir Woods, but otherwise the population appears to primarily consist of adults. Three aggressive interactions between Spotted and Barred owls were recorded. They also note observations of Barred Owls foraging in streams hunting for crayfish (*Pacifastacus* spp.) and foraging while walking on the ground.

Johnson, N.K. 1994. Pioneering and natural expansion of breeding distributions in western North American birds. *Studies in Avian Biology* 15:27-44.

The author discusses the possible causes for the range expansions of a number of species, the Barred Owl among them. The author speculates that this species' expansion may reflect a natural ebb and flow at the range margins and thus reclaiming ground occupied in the past. Another factor may be related to climate change, in that this species in the east is typified by wet summers and high humidity, and the western United States has become warmer and wetter when comparing 1921-1954 to 1956-1977 and from the mid-1970s to mid-1980s.

Jones, J.E. and A.J. Kroll. 2016. A joint model of species interaction dynamics for multistate processes incorporating imperfect detection. *Ecosphere* 7(10):e01477.10.1002/ecs2.1477.

The authors present a model of across-season species interaction dynamics with multistate processes for dominant and subordinate species while incorporating imperfect species detection, which had been a concern with earlier modelling efforts. They demonstrate this model using data from a long-term study in Oregon, evaluating interactions between the

Northern Spotted Owl and Barred Owl, with the latter species considered to be dominant for the model. Their results suggest that Barred Owls are associated with declines in Spotted Owl forming pairs, but not necessarily occupancy. Estimated counts of occupied Barred Owl territories doubled over the 10-year span, while Spotted Owl pair territories declined by 1.3 territories per year. Though there appears to be a rise in unoccupied and single-occupied Spotted Owl territories, the posterior credible intervals contained zero, indicating uncertainty in the trend direction.

Keane, J.J. 2014. California Spotted Owl. Pages 437–467 in: J.W. Long, L. Quinn-Davidson, and C.N. Skinner, eds. Science synthesis to promote resilience of social-ecological systems in the Sierra Nevada and southern Cascades. Gen. Tech. Rep. PSW-GTR-247. U.S.D.A. Forest Service, Pacific Southwest Research Station, Albany, CA.

The author describes the threat of Barred Owls as an “Additional Ecological Stressor” for the California Spotted Owl, due to its expansion into the range of that subspecies. He reviews the literature of its impact on the Northern Spotted Owl as it invaded their range over the last 40 years. He notes that to date a total of 73 Barred Owls and hybrids have been detected in the Sierra Nevada. He believes that Barred Owl numbers are likely higher than documented in the Sierras, as there has been no systematic surveys for them to date and species-specific survey methods are required to account for differences between Spotted and Barred owls.

Keane, J.J. 2017. Chapter 7: Threats to the viability of California Spotted Owls. Pages 185-238 in: R.J. Gutiérrez, P.N. Manley, and P.A. Stine, tech. eds. The California Spotted Owl: current state of knowledge. Gen. Tech. Rep. PSW-GTR-254. U.S.D.A. Forest Service, Pacific Southwest Research Station, Albany, CA.

After reviewing the threats currently listed in the California Spotted Owl Technical Assessment, the author outlines several new threats that have emerged since that 1992 assessment including the invasion of the Barred Owl. He notes that the Barred Owl is considered a primary threat to the Northern Spotted Owl and they are currently expanding their range into the Sierra Nevada range. He reviews recent literature describing the impact of the invader on the Northern Spotted Owl. No formal surveys had been conducted for Barred Owls in the range of the California Spotted Owl. He reviews incidental sightings of a total of 51 Barred Owls and 27 hybrids that had been detected in the Sierra Nevada between 1989 and 2013. He suggests that without control efforts, Barred Owls can potentially become a primary threat to the California Spotted Owl in the Sierra Nevada.

Kelly, E.G. 2001. The range expansion of the Northern Barred Owl: An evaluation of the impact on Spotted Owls. M.S. Thesis, Oregon State University, Corvallis, Oregon. 78 p.

The author characterizes Barred Owl distribution and population increase in Oregon, investigates Spotted Owl territory performance before and after Barred Owl detection, and documents cases of hybridization between Barred Owls and Spotted Owls. When Barred Owls were detected within 0.80 km of a Spotted Owl territory center, 85% of Spotted Owls moved

>0.80 km or disappeared completely. In comparison, at territories without Barred Owls, 32% of Spotted Owls moved >0.80 km or disappeared.

Kelly, E.G., and E.D. Forsman. 2004. Recent records of hybridization between Barred Owls (*Strix varia*) and Northern Spotted Owls (*S. occidentalis caurina*). *Auk* 121:806–810.

The authors summarized records of hybridization between Barred Owls and Northern Spotted Owls in Washington and Oregon through 1999, from surveys and >9,000 banding records in 1970-1999. The authors report on both F1 and F2 individuals and their parentage, if known. They found hybridization at 28 locations. A total of 47 hybrids were recorded. They conclude that there is little evidence that hybridization will be a serious threat to either species, given the low number of hybrids compared to the high numbers surveyed and banded.

Kelly, E.G., E.D. Forsman, and R.G. Anthony. 2003. Are Barred Owls displacing Spotted Owls? *Condor* 105:45–53.

By 1998, there were an estimated 706 Barred Owl territories in Oregon state, while between 1987 and 1998, Spotted Owl demographic study areas in Oregon and Washington showed significant increases in the percentage of Spotted Owl territories with Barred Owl detections. The authors found that for territories with Barred Owls close to the territory center (within 0.8 km), Spotted Owl occupancy scores declined. By contrast, if Barred Owls were further away, occupancy scores were only slightly less than those where no Barred Owls were detected. The authors noted that even though occupancy scores went down when Barred Owls were close to Spotted Owl territory centers, it did not necessarily lead to displacement, as some pairs of Spotted Owls persisted (or new ones arrived) at territories where Barred Owls had been detected near the territory center.

Knopf, F.C. 1994. Avian assemblages on altered grasslands. Pages 247-254 in J.R. Jehl and N.K. Johnson, Eds. *A century of avifaunal change in western North America. Studies in Avian Biology* 15.

The author discusses changes in habitat across the grasslands that may have enabled the Barred Owl to expand to the west coast, such as an increase in tree plantings and ecological invasions. This consists of fire control which enabled woody vegetation on the northern grasslands and planting of shelterbelts to reduce wind erosion. There has also been development of streamside forests of alien and exotic tree species across the western landscape due to water management practices favoring woody colonization and secondary succession.

Kroll, A.J., T.L. Fleming, and L.L. Irwin. 2010. Site occupancy dynamics of Northern Spotted Owls in the eastern cascades, Washington, USA, 1990–2003. *Journal of Wildlife Management* 76:1264–1274.

Between 1990 and 2003, Spotted Owl detection probabilities decreased for both individuals and pairs if Barred Owls were detected. For all Spotted Owls, both singles and pairs, site occupancy probabilities declined moderately during the study. The authors explored the effect of Barred Owls on detection probabilities, local extinction, colonization, and occupancy

probabilities of Spotted Owls. The authors concluded that apparent losses of resident, territorial owls were not balanced by new owls, either through in situ recruitment or immigrants, as annual site occupancy probabilities declined from 1990 to 2003.

Kroll, A.J., J.E. Jones, A.B. Stringer, and D.J. Meekins. 2016. Multistate models reveal long-term trends of Northern Spotted Owls in the absence of a novel competitor. *PlosOne* 11(4): e0152888. DOI: 10.1371/journal.pone.0152888.

The authors used a multistate model to evaluate Northern Spotted Owl territory occupancy and reproductive dynamics in an area which has not been invaded by Barred Owls as of 2014, in Mendocino County, California. They did not find evidence to indicate that territory occupancy by Northern Spotted Owl pairs had declined substantially over a 25-year period, but rather had remained relatively constant.

Lesmeister, D.B., R.J. Davis, P.H. Singleton, and J.D. Wiens. 2018. Chapter 4: Northern Spotted Owl habitat and populations: Status and threats. P. 245-298 in T.A. Spies, P.A. Stine, R.A. Gravenmier, J.W. Long, M.J. Reilly. 2018. Synthesis of science to inform land management within the Northwest Forest Plan area. Gen. Tech. Rep. PNW-GTR-966. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 1020 p., 3 vol.

Summary of the current knowledge of the Northern Spotted Owl's habitat, population status, and threats to the population. They first review the history of the owls' status at the time of the creation of the Northwest Forest Plan (NWFP), and that the implementation of the NWFP had a positive effect on demographic values as reported in 2006. They summarize how the Spotted Owl population continues to decline, with the annual rates of decline accelerating in many areas. The threats of Barred Owls to the population are outlined and discussed, including lower Spotted Owl territory occupancies, survival and reproduction is lower, and hybridization between the species is increased, as well as that Barred Owls can directly alter Spotted Owl behavior. Other threats to Spotted Owls are discussed, including habitat disturbance, climate change, and environmental contaminants.

Lesmeister, D., C. McCafferty, K. Beerweiler, S. Kukar, N. Lerro, B. Mason, B. Meiering, K. Skybak, A. Thomas, and K. Wert. 2016. Demographic characteristics of Spotted Owls in the Oregon Coast Ranges, 1990-2015. Annual research report. USDA Forest Service, Pacific Northwest Research Station, Corvallis, OR and Dept. of Fish and Wildlife, Oregon State Univ., Corvallis, OR. 18 p. <https://reo.gov/monitoring/reports/nso/COA%20nso%20demog%20annual%20report%202015.pdf>. Last accessed 7/30/2018.

The authors detail research accomplishments for the 2015 fiscal year in the Oregon Coast Ranges study area and summarize the demographic characteristics for the length of the study from 1990-2015. They include a summary of incidental detections of Barred Owls by site which has increased to 89% of the historic territories in 2015. An appendix lists an annual

summary of the number of sites surveyed and all Barred, Spotted, and hybrid *Strix* owls detected.

Lewicki, K.E., K.P. Huyvaert, A.J. Piaggio, L.V. Diller, and A.B. Franklin. 2015. Effects of Barred Owl (*Strix varia*) range expansion on *Haemoproteus* parasite assemblage dynamics and transmission in Barred and Northern Spotted Owls (*Strix occidentalis caurina*). *Biological Invasions* 17:1713–1717.

The authors compared *Haemoproteus* blood parasite assemblages among Northern Spotted Owls in their native range and Barred Owls in both their native (eastern) and invasive (western) ranges to evaluate predictions of hypotheses about parasites and biological invasions. The results showed the most support for the Enemy Release Hypothesis, where hosts benefit from a loss of parasites in their invasive range, since the western Barred Owls were less likely to be infected than eastern Barred Owls, and had a lower haplotype diversity. Northern Spotted Owls had higher parasite diversity and probability of infection than sympatric Barred Owls, offering some support for the Parasite Spillover (invasive hosts act as new reservoir to native parasites) and Dilution Effect (invasive species act as poor host to native parasites and decrease density of potential hosts in the invaded range) hypotheses.

Livezey, K.B. 2007. Barred Owl habitat and prey: A review and synthesis of the literature. *Journal of Raptor Research* 41:177–201.

The author reviews current literature for information on habitat and prey for the Barred Owl across its eastern and western ranges. He includes three comparison studies with Spotted Owls. Barred Owl sites were significantly lower in elevation and flatter sloped in Washington study sites than for Spotted Owls, however one study showed that Barred Owls increased their number and began extending their distribution farther up valleys and higher in elevation. Most studies found Barred Owl sites were situated close to water. Barred Owl sites contained significantly less old forest within 0.8 km of site centers than Spotted Owls and site centers were located in significantly younger stands. The authors gathered diet data from studies using pellets and other data collection methods. Barred Owls in the west ate more amphibians and fewer crayfish than in the east.

Livezey, K.B. 2009a. Range expansion of Barred Owls, part I: Chronology and distribution. *American Midland Naturalist* 161:49–56.

The author presents new records of Barred Owls on their expansion westward, and proposes a new expansion route through the northern United States instead of southern Canada as proposed by all other earlier literature sources. He proposes that Barred Owls moved west along the Missouri River into central North Dakota and along the Yellowstone and Musselshell rivers in east-central Montana in the 1870s, which is earlier than the earliest western Canada records in the 1930s and 1940s. They then expanded northeast into Canada (encountering the later, separate western expansion from Manitoba), and northwest to British Columbia, where they eventually spread south through the western United States.

Livezey, K.B. 2009b. Range expansion of Barred Owls, part II: Facilitating ecological changes. *American Midland Naturalist* 161:323-349.

The author evaluates the plausibility of five ecological changes proposed in literature to have facilitated the westward range expansion of Barred Owls. He adapted strength-of-evidence criteria to score those ecological changes as they relate to Barred Owls: (1) cold temperature; (2) lack of forests in the Great Plains; (3) avian predators; (4) lack of fragmentation in western forests; and (5) need to adapt to western forests. He found the only plausible ecological change was an historical lack of trees in the Great Plains. The advent of European settlers allowed increases in forests by excluding fires, both historically set by Native Americans or wildfires, and planting trees. Large portions of the plains reverted back to forests as early as the mid-1800s. Without fires, trees invaded the prairies with as little of 20-40 years without fires. To a lesser degree, extirpation or drastically reducing numbers of native grazers (bison, elk, and deer) and in some areas extirpating beavers also contributed to the increase in forests. He posits that Barred Owl range expansion was prohibited for millennia by actions of Native Americans and recently facilitated by actions of European settlers.

Livezey, K.B., M.F. Elderkin, P.A. Cott, J. Hobbs, and J. P. Hudson. 2008. Barred Owls eating worms and slugs: The advantage in not being picky eaters. *Northwestern Naturalist* 9:185-190.

Barred Owls were observed in Nova Scotia and British Columbia, Canada, eating earthworms and bringing them back to nestlings. One owl was observed eating slugs in a meadow in Olympic National Park, Washington, USA. The authors discuss the difficulties in detecting such soft-bodied prey in diet studies that rely on regurgitated pellets, and suggest that such soft-bodied prey could account for a larger proportion of their diet than previously understood. They also discuss possible implications for dietary overlap with Spotted Owls.

Livezey, K.B. and T.L. Fleming. 2007. Effects of Barred Owls on Spotted Owls: The need for more than incidental detections and correlational analyses. *Journal of Raptor Research* 41(4):319-325.

The authors review the current state of Barred Owl research in areas of sympatry with the Spotted Owl, noting most studies have relied on incidental data collected during Spotted Owl surveys and only four studies directly collected data on Barred Owls. They argue that the exclusive use of incidental surveys: 1) confines analyses to correlation; 2) could result in under detection of Barred Owls; and 3) limits surveys to areas in which Spotted Owls are being surveyed, resulting in the failure to detect Barred Owls in other areas. They recommend a potential areas of research focused on Barred Owls and the effects of Barred Owls on Spotted Owls, including Barred Owl detectability, gathering basic Barred Owl ecological data, studying interactions between the species, and conducting Barred Owl removal experiments.

Mazur, K.M. and P.C. James. 2000. Barred Owl (*Strix varia*), *The Birds of North America* (P.G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: <https://birdsna.org/Species-Account/bna/species/brdowl>. DOI: 10.2173/bna.508. Last accessed 7/30/2018.

In the introduction to this compendium of information about the Barred Owl, the authors describe the historical range expansion from the east coast through boreal forests of Canada into the Pacific Northwest of Canada and the United States. They note that this brought the species into contact with the closely-related Spotted Owl and, as they stated, that the more aggressive Barred Owl has been known to displace and hybridize with the Spotted Owl, a further threat to that already endangered species. Although the Barred Owl is associated almost exclusively with large trees in old growth forests on the east coast, it apparently is more adaptable in the west and readily inhabits mature second-growth forest as well. The authors also describe the diet of the Barred Owl.

Monahan, W.B., and R.J. Hijmans. 2007. Distributional dynamics of invasion and hybridization by *Strix* spp. in western North America. *Ornithological Monographs* 63: 55-66.

The authors investigated the geographic and environmental characteristics of invasion and hybridization of the Barred Owl with the Spotted Owl. They note that the Barred Owl's first contact with the Northern Spotted Owl was in southwestern Canada around 1973. From there, it continued to expand south and now is also in the California Spotted Owl's range. They examined the possibility of warming temperatures as an origin for the Barred Owl's invasion. Temperatures began to rise in the early part of the 20<sup>th</sup> century, with an increase mean temperatures along the expansion corridor as compared to their original territory, while there was no change in precipitation. They considered that the range expansion was natural because of this temperature change, that the expansion corridor reflected similar habitat to that in their eastern range, and there was suitable habitat in the west for them to colonize. They found hybrids were randomly distributed similar to the parental species.

Olson, G.S., R.G. Anthony, E.D. Forsman, S.H. Ackers, P.J. Loschl, J.A. Reid, K.M. Dugger, E.M. Glenn, and W.J. Ripple. 2005. Modeling of site occupancy dynamics for Northern Spotted Owls, with emphasis on the effects of Barred Owls. *Journal of Wildlife Management* 69:918-932.

The authors modelled the site occupancy dynamics of Spotted Owls in three study areas in central-coastal Oregon from 1990-2002, including the effect of the presence of Barred Owls which were recorded incidentally to surveys. Since Barred Owls were first seen in 1990, there was a modest increase of the proportion of sites with Barred Owls present in two of three study sites. The authors explored the effect of Barred Owls on detectability, local extinction, and colonization probabilities. Barred Owls negatively affected Spotted Owl detectability, as well as local-extinction and colonization probabilities. Barred Owl effects on site occupancy varied by study area and levels of occupancy (Spotted Owl individual or pair).

Olson, G.S., E.M. Glenn, R.G. Anthony, E.D. Forsman, J.A. Reid, P.J. Loschl, and W.J. Ripple. 2004. Modeling demographic performance of Northern Spotted Owls relative to forest habitat in Oregon. *Journal of Wildlife Management* 68:1039-1053.

The authors developed statistical models relating Spotted Owl survival and productivity to forest cover types within the Roseburg Study Area in the Oregon Coast Range. They included presence of Barred Owls among the covariates for this model. They found that Spotted Owl reproductive rates were at least in part negatively influenced by the presence of Barred Owls. Models for survival and habitat fitness potential did not include Barred Owl effects.

Pearson, R.R. and K.B. Livezey. 2003. Distribution, numbers, and site characteristics of Spotted Owls and Barred Owls in the Cascade Mountains of Washington. *Journal of Raptor Research* 37:265–276.

The authors summarized the population and site characteristics for Spotted and Barred owls in the Gifford Pinchot National Forest, Washington, study area from 1978 to 2001. The percent of Barred Owls relative to all *Strix* detections increased significantly annually through the study and did not appear to be leveling off. Site centers for both species were lower in elevation than random, though Spotted Owl sites were significantly higher in elevation than those of Barred Owls. The mean age of forest stand at Spotted Owl site centers was significantly greater than for Barred Owls. The number of Barred Owl sites approached or surpassed the number of occupied Spotted Owl sites in Land Use Allocation areas specifically allocated to benefit Spotted Owls (critical habitat units and late successional reserves).

Pearson, R.R. and K.B. Livezey. 2007. Spotted Owls, Barred Owls and Late-successional Reserves. *Journal of Raptor Research* 41(2): 156-161.

The authors compared Barred and Spotted Owl territory numbers among Late-successional Reserves (LSRs) and non-reserve lands in the study area. Four of five LSRs contained more Barred Owl than Spotted Owl sites; by contrast, non-reserve areas contained more Spotted Owl than Barred Owl sites. One LSR which was low-elevation with flat terrain had the highest density of Barred Owl sites than the other LSRs, and few Spotted Owl sites. The one LSR which went against the trend was high-elevation with steep terrain and had only Spotted Owl sites. They suggest that these local factors favored Spotted Owls over Barred Owls and that a natural balance may have been achieved which allow the coexistence of these species.

Perlman, K.R. 2017. Using a two-species individual-based model to examine the population responses of Northern Spotted Owls to experimental removals of Barred Owls in the Pacific Northwest. M.S. Thesis, Oregon State University, Corvallis, OR. 92 p.

The author explored the response of Spotted Owl populations to simulated Barred Owl removals in four demographic study areas (Cle Elum, Coast Range, Klamath, and Hoopa) using two-species individual-based models. A percentage of territorial Barred Owls were removed each year. If no removals were implemented, all Northern Spotted Owl populations go extinct within the 100-year simulation. The results of removals differed by study area and removal intensity. In most areas, removal of 25% of Barred Owls led to local extinction or a dramatic decrease of Spotted Owls. The best results were in Cle Elum, where populations increased under most removal intensities. In Klamath and Hoopa, all removal intensities resulted in some decrease in Spotted Owl populations. In no scenario did owl populations

return to pre-invasion levels. When Barred Owl removals were implemented on local Barred Owl populations at steady-state, as was observed in the Cle Elum and Coast Range removal area simulations, the local Northern Spotted Owl population exhibits higher likelihood of stabilizing or recovering in the long-term. Conversely, when Barred Owl removals were implemented on local populations that were still growing or just beginning to reach steady-state, as seen in the Klamath and Hoopa removal areas, local Northern Spotted Owl populations decline or reach local extinction in the long-term.

Schilling J.W., K.M. Dugger, and R.G. Anthony. 2013. Survival and home-range size of Northern Spotted Owls in southwestern Oregon. *Journal of Raptor Research* 47(1):1–14.

The authors estimated monthly survival rates and home-range sizes in relation to habitat characteristics for Northern Spotted Owls in the Rogue River-Siskiyou National forest. They included the presence of Barred Owls in their analysis, but found no influence of Barred Owls on Spotted Owl survival during the study. They hypothesized this was because they did not measure their Barred Owl covariate on a fine enough temporal scale to model monthly survival rates of Spotted Owls.

Singleton, P.H. 2015. Forest structure within Barred Owl (*Strix varia*) home ranges in the eastern Cascade Range, Washington. *Journal of Raptor Research* 49(2): 129-140.

The author analyzed breeding and nonbreeding habitat used by 14 radio-tagged Barred Owls from March 2004 to September 2006 in the eastern Cascade range of Washington state. He found that forest structure characteristics used by Barred Owls in this study were within the range of conditions reported to be used by Spotted Owls in this area.

Singleton, P.H., J.F. Lehmkuhl, W.L. Gaines, and S.A. Graham. 2010. Barred Owl space use and habitat selection in the Eastern Cascades, Washington. *Journal of Wildlife Management* 74:285-294.

The authors quantify space-use patterns of Barred Owls, identify factors in their habitat selection, and model those factors and relative use by Barred Owls in the eastern Cascades of Washington state. They found that Barred Owls were associated with moist, structurally diverse, closed canopy forests on gentle slopes. They did not find a strong association with proximity to water. Forest structural characteristics for Barred Owls were similar to those reported for Spotted Owls. Spotted Owl mean home ranges were approximately 8 times larger than that of Barred Owls.

Sovern, S.G, E.D. Forsman, G.S. Olson, B.L. Biswell, M. Taylor, and R.G. Anthony. 2014. Barred Owls and landscape attributes influence territory occupancy of Northern Spotted Owls. *Journal of Wildlife Management* 78(8):1436-1443. DOI: 10.1002/jwmg.793

The authors used territory occupancy modeling to assess the probabilities of local colonization and local extinction of Northern Spotted Owls in territories in Washington State, in relationship to habitat variables and presence of Barred Owls. Data for the analyses were from Spotted Owl

surveys, recording all owls that responded, including Barred Owls. The presence of Barred Owls was positively related to extinction probability, suggesting that because of competition with Barred Owls, Spotted Owls are being displaced. Barred Owls did not influence colonization probabilities. Barred Owls were negatively related to detection probability of Spotted Owls. The authors suggested that the latter could be an indication that Spotted Owls may be modifying their calling behavior in the presence of Barred Owls.

Van Lanen, N.J., A.B. Franklin, K.P. Huyvaert, R.F. Reiser II, and P.C. Carlson. 2011. Who hits and hoots at whom? Potential for interference competition between Barred and Northern Spotted owls. *Biological Conservation* 144:2194–2201.

The authors used a playback experiment in the field with mounted owl taxidermy mounts to explore inter- and intraspecific reactions and quantify aggressive vocal and physical behavior between Spotted and Barred owls during territorial defense. All playbacks were focused on male responses. Barred Owls responded with higher levels of vocal and physical aggression than Northern Spotted Owls in interspecific interactions. This suggested that Barred Owls are more likely to be the dominant species. However, when head attacks connected, Spotted Owls struck the taxidermy mounts with a greater capacity to cause head injury compared to Barred Owls. Spotted Owls were more likely to call aggressively and attack when presented with a conspecific mount and call than a Barred Owl.

Wasser, S.K., L.S. Hayward, J. Hartman, R.K. Booth, K. Broms, J. Berg, E. Seely, L. Lewis, and H. Smith. 2012. Using detection dogs to conduct simultaneous surveys of Northern Spotted (*Strix occidentalis caurina*) and Barred Owls (*Strix varia*). *PlosOne* 7(8): e42892.

The authors describe a method for surveying for Barred and Northern Spotted owls using detection dogs. Dogs searched for owl droppings which were later identified by mitochondrial DNA. Detection probabilities for both owl species were significantly higher using dogs than for vocalization surveys. Detection probabilities also increased with an increase in number of surveys conducted per polygon. By a third visit, the DNA-confirmed cumulative detection probability of dog surveys was 28% higher for dog surveys than after six visits for vocalization surveys. Since it has been found that Barred Owl presence can suppress Northern Spotted Owl responsiveness to vocalization surveys, this may be a new, reliable method to aid in establishing occupancy of owls without requiring owl vocalization.

Weisel, L.E. 2015. Northern Spotted Owl and Barred Owl home range size and habitat selection in coastal northwestern California. M.S. Thesis, Humboldt State University, Arcata, CA. 60 p.

Home range sizes for Northern Spotted and Barred owls were not significantly different from each other in breeding or non-breeding seasons. Both used larger home ranges in the non-breeding season than the breeding season. Spotted Owls occupied smaller home ranges in northern California than in the northern portion of their range. Both species exhibited habitat selection for understory vegetation, hardwood trees, and distance to nest. Also, there was

indication that interaction with the conspecific owl was also a factor, indicating some degree of resource partitioning.

Wiens, J.D. 2012. Competitive interactions and resource partitioning between Northern Spotted Owls and Barred Owls in western Oregon. Ph.D. Thesis: Oregon State University, Corvallis, OR. 141 p.

Home ranges for Spotted Owls were 2-4 times larger than those of Barred Owls. Barred Owls nested closer to Spotted Owl activity centers than to those of other Barred Owls. There was a positive relationship between Spotted Owl home range size and the presence of Barred Owls, but not for Barred Owls and Spotted Owl presence. While they found little intraspecific home range overlap, there was considerable interspecific home range overlap. The probability of locating a Spotted Owl in a Barred Owl home range was considerably lower than locating a Barred Owl in a Spotted Owl's home range. Newly colonizing Barred Owls were highly likely to be found within the breeding ranges of Spotted Owls. In these cases, interspecific territorial interactions were regularly seen, including agitated vocalizations by both species near nest sites, and Barred Owls chasing Spotted Owls out of shared core-use areas.

Wiens, J.D., R.G. Anthony, and E.D. Forsman. 2011. Barred Owl occupancy surveys within the range of the Northern Spotted Owl. *Journal of Wildlife Management* 75:531-538.

The authors investigated behavior, detection probabilities and landscape occupancy patterns of Barred Owls. They found that Barred Owl response rates to Spotted Owl tapes were lower than for Barred Owl tapes, thus the numbers of Barred Owls detected by Spotted Owl surveyors may be underestimated. As well, Barred Owls showed a higher prevalence of silent approaches during Spotted Owl surveys, which could also decrease detections and therefore estimates of Barred Owls. Barred Owls may only be detected in the last 5 minutes of a 15-minute Barred Owl survey, so Spotted Owl surveys that use shorter survey times of 10 minutes may not detect them. The authors recommend that Spotted Owl surveys be extended to at least 15 minutes and additional training.

Wiens, J.D., R.G. Anthony, E.D. Forsman. 2014. Competitive interactions and resource partitioning between Northern Spotted Owls and Barred Owls in Western Oregon. *Wildlife Monographs* 185:1-50.

Spotted and Barred owls were radio-tagged and followed for two seasons, in addition to targeted surveying for both species. Home ranges and core-use areas of Spotted Owls were 2-4 times that of Barred Owls; some Barred Owl territories were completely subsumed by a Spotted Owl territory. Spotted Owls spent more time foraging on steep slopes in ravines dominated by old conifer trees than Barred Owls which used available forest types more evenly and areas along relatively flat areas along streams. Otherwise, habitat use patterns were similar. Spotted Owl diet consisted primarily of mammals while Barred Owls depended less on mammals and included birds, frogs, and insects. Barred Owls were more successful demographically, with a higher annual survival and producing more young per pair. For Spotted Owls, the number of young produced increased linearly with increasing distance from a territory center of a pair of Barred Owls.

Wiens, J.D., K.M. Dugger, K.E. Lewicki, and D.C. Simon. 2017. Effects of experimental removal of Barred Owls on population demography of Northern Spotted Owls in Washington and Oregon—2016 progress report: U.S. Geological Survey Open-File Report 2017-1040, 23 p. <https://doi.org/10.3133/ofr20171040>. Last accessed 7/30/2018.

In March 2015, the authors began a 5-year study in Washington and Oregon to remove Barred Owls by lethal methods, primarily during the nonbreeding season. They report here on their early results. During the second season of owl removal, a substantially greater proportion of territorial subadults were collected at sites where established resident adult pairs had been removed in the previous months. This occurred fairly quickly, suggesting that these younger birds were available within the treated landscape to quickly fill in vacancies created by removals. In the Cle Elum study area, there was a decline of 24-25% in probability of use by Barred Owls on both the treated and untreated areas – indicating there may be some other reason behind the decline than removal activities. In the Coast Ranges study area, there was a decline in probability of use of territories by Barred Owls in the treatment area by 13% after removal.

Yackulic, Charles B. 2017. Competitive exclusion over broad spatial extents is a slow process: evidence and implications for species distribution modeling. *Ecography* 40(2): 305–313.

The authors discuss the role of competitive exclusion in shaping species distributions over broad spatial extents by reviewing ecological literature and reanalyzing data through simulations based on previously published parameter estimates from studies of competition among Northern Spotted and Barred owls. These simulations estimate an equilibrium expectation that Northern Spotted Owls will be extirpated from most or all of their geographic range. Competition would initially increase local extinction rates for the Spotted Owl, which would lower its occurrence rates, which in turn would lower colonization rates. It would take from 9 to 16 years for Barred Owls to reach levels similar to equilibrium predictions (>90% of territories). In contrast, it may take from 40 years to centuries (median 88 years) for Spotted Owls to be extirpated from all or most of the region.

Yackulic, C.B., J. Reid, R. Davis, J.E. Hines, J.D. Nichols, and E. Forsman. 2012. Neighborhood and habitat effects on vital rates: Expansion of the Barred Owl in the Oregon Coast Ranges. *Ecology* 93(8):1953-1966.

The authors use dynamic occupancy models to explore the importance of neighborhood effects (regional occupancy) and habitat covariates in determining colonization and extinction rates for Barred Owl in western Oregon. They found that regional occupancy influences colonization and extinction rates and that habitat plays an important role in determining colonization and extinction rates. In particular, colonization is higher and extinction is lower in survey polygons with more riparian forest, with the effects of riparian forest being greater on extinction rates than on colonization rates. They suggest that understanding the influence of regional occupancy on colonization and extinction rates of Barred Owls will be of importance in

predicting the impacts of Barred Owl removal as a management tool. They suggest that removal at the scale of individual survey polygons may have little impact on regional estimates of occupancy.

Yackulic, C.B., J. Reid, J.D. Nichols, J.E. Hines, R. Davis, E. Forsman. 2014. The roles of competition and habitat in the dynamics of populations and species distributions. *Ecology* 95(2):265–279.

The authors analyzed data from a two-decade (1990-2010) study on Northern Spotted Owls, and modeled the interactive effects of an invader species (Barred Owl) on the resident species (Northern Spotted Owl). Local extinction probability increased for both species when the other was present, but the effect was greater for the Spotted Owl. The effects of the invader also led to a weaker correlation of habitat preferences in the resident species. Their analysis showed that competition is likely to exclude the resident species, both through its immediate effects on local extinction and indirectly by lowering colonization rates. Future forecasting suggested that Spotted Owl numbers will be depressed, but not likely completely excluded; however the population may decrease below sustainable population levels – over half of the model simulations fell to fewer than 25 pairs over the following 25 years in the study area when Barred Owls were in the equation.

Zipkin, E.F., S. Rossman, C.B. Yackulic, J.D. Wiens, J.T. Thorson, R.J. Davis, and E.H. Campbell Grant. 2017. Integrating count and detection–nondetection data to model population dynamics. *Ecology* 98(6):1640–1650.

The authors present a modeling framework for integrating detection–nondetection and count data into a single analysis to estimate population dynamics, abundance, and individual detection probabilities during sampling. They demonstrate this model using existing detection–nondetection (1996-2014) and count (2015-2016) data for Barred Owls in the Pacific Northwest to examine the factors influencing population abundance over time. Model results showed that the Barred Owl population grew over time, with high annual survival probabilities ranging from 0.86-0.93, which increased with the amount of older coniferous forest cover. Colonization rates increased from 0.14 to 0.90 from 1996 to 2016. This model may be used to incorporate historical and citizen science data into demographic analyses.

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**Appendix A.** Northern Spotted Owl study areas and codes used for identification for Table 3 and Figure 4, Dugger et al. (2016).

<b>Study area</b>	<b>Study area code</b>
Washington	
Cle Elum	CLE
Rainier	RAI
Olympic	OLY
Oregon	
Coast Ranges	COA
H. J. Andrews	HJA
Tyee	TYE
Klamath	KLA
South Cascades	CAS
California	
Northwest California	NWC
Hoopa	HUP
Green Diamond Resources	GDR
Control before removal	GDR-CB
Treatment before removal	GDR-TB
Control after removal	GDR-CA
Treatment after removal	GDR-TA