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Review

Review of the Effects of Barred Owls on Spotted Owls

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ABSTRACT Barred owls (*Strix varia*) are forest-dwelling owls, native to eastern North America, with populations that expanded westward into the range of the spotted owl (*Strix occidentalis*). Barred owls exert an overwhelmingly negative influence on spotted owls, thereby threatening spotted owl population viability where the species co-occur. In this review, we provide an overview of the barred owl's range expansion and detail and synthesize previously published literature on spotted and barred owls within the range of the spotted owl as related to potential future outcomes for the northern spotted owl (*S. o. caurina*). We include research on diet, habitat use and selection, effects of barred owls on spotted owl demography and behavior, hybridization with spotted owls, parasites, contemporary management, and future research needs for spotted owl populations given continued barred owl expansion throughout western North America. Our literature review and synthesis should provide managers with the information necessary to develop strategies that mitigate deleterious effects of barred owls at local and landscape scales. © 2019 The Wildlife Society.

KEY WORDS barred owl, endangered species, forest, invasive species, spotted owl, *Strix occidentalis*, *Strix varia*, western United States.

Barred owls (*Strix varia*) and spotted owls (*Strix occidentalis*) are large, forest-dwelling avian predators. Although barred and spotted owls rely on forested landscapes, the barred owl exhibits a more diverse diet (i.e., consuming mammals, birds, fish, amphibians, reptiles, invertebrates; Mazur and James 2000) compared to spotted owls that specialize on mammalian prey (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 species co-occur, the continuing expansion of barred owls into the range of the northern (*S. o. caurina*) and California spotted owls (*S. o. occidentalis*) has presented emergent and difficult challenges for wildlife managers (Gutiérrez et al. 2004, Keane 2014).

In this paper, our objective was to summarize the existing published research on barred owls within the range of the spotted owl. First, we present an overview of barred owl expansion from its historical range in eastern North America into the range of the spotted owl, and review population trajectories of the barred owl in the west. Next, we used an outline of 9 hypothetical futures for spotted and barred owl populations from Gutiérrez et al. (2004) to explore findings from research in support or opposition of each hypothesis. We detailed, compared, and contrasted the 2 species' diets, habitat use, and habitat selection; effects of barred owls on spotted owl demography and behavior; shared parasites; and hybridization with spotted owls. We also examined current and potential future management strategies for barred and spotted owls. Lastly, we identified future research priorities. Broadly, we reviewed and synthesized current research for investigators and managers to help develop strategies for the management of spotted owl and recently arrived barred owl populations in western North America.

METHODS

We gathered relevant literature for this review using Google Scholar (Google Scholar, https://scholar.google.com/, accessed 22 Aug 2017) and Web of Science search engines (https://apps.webofknowledge.com/, accessed 22 Aug 2017). Search terms included barred owl, spotted owl, *Strix occidentalis*, *Strix varia*, behavior, competition, conservation, controversy, demography, detectability, diet, ecology, extinction, habitat, hybrid, invasion, invasive species, occupancy, populations, prey, range expansion, removal, and territories.

To document the westward expansion of the barred owl, we gathered locations and dates of early barred owl sightings through 2 main sources: 1) literature located using the online search engines and 2) sightings recorded by the public into eBird, which are displayed and retrievable through an online

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map of current and historical barred owl locations (eBird 2019; Fig. 1). Search terms included barred owl, range expansion, first records, British Columbia, Washington, Oregon, and California. We mapped locations into Google Earth (Google Earth Pro 7.3.2.5776, https://www.google.com/earth/, accessed 22 Apr 2019) using location descriptions from the citation (e.g., Wildcat Campground, Oregon; Forest Ranch, Butte County, California) or geolocations if available. We annotated locations with descriptions and citations for each sighting. Most locations consisted of ≥1 owl observed at a single site, with the exception of records from spotted owl researchers documenting the first barred owls in their study areas, which may have consisted of several barred owls on several territories. Our intent was to document the expansion of barred owls into the range of the spotted owl, and therefore did not include numerous historical locations east of the Rocky Mountain range in their earliest western expansion (Livezey 2009*a*). We saved the final map as a Google Map keyhole markup language (KML) file.

RESULTS

Westward Expansion of the Barred Owl and Current Populations

Before the second half of the last century, ranges of the spotted owl and barred owl did not overlap, except in areas of Mexico. The spotted owl occupied western and southwestern North America (Gutiérrez et al. 1995), the barred owl occupied eastern North America (Mazur and James 2000), and the Great Plains divided the 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 2009*a*). 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;

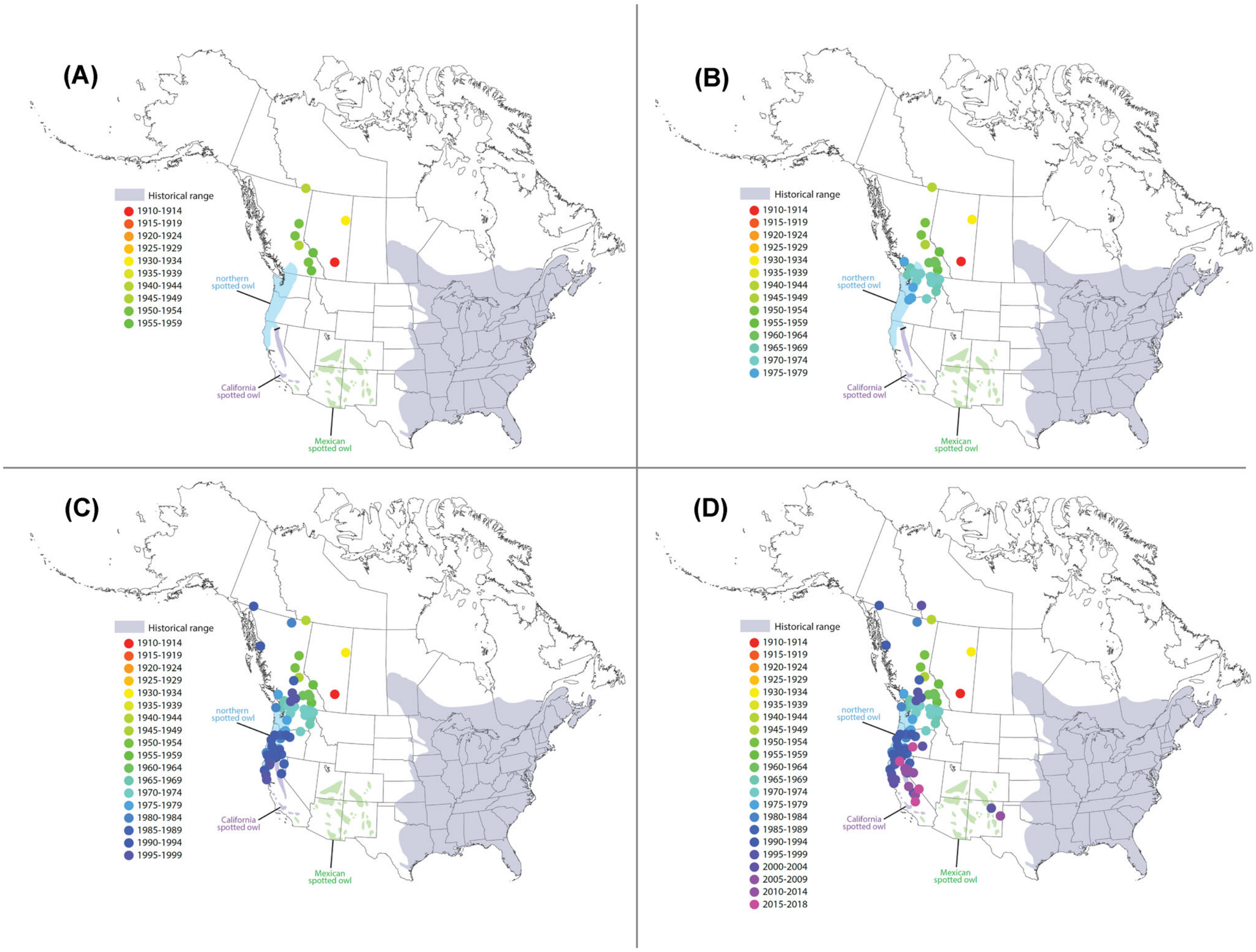

Figure 1. Range expansion of the barred owl from its historical range (gray shading) into western North America. Dots show individual sightings of ≥1 barred owls. To better illustrate invasion dynamics of barred owls throughout western North America, we provide observations in 20-year increments, beginning in 1910 through 1959 shown on panel A, demonstrating the advance of barred owls into the delineated ranges of northern, California, and Mexican spotted owls. A) 1910–1959, data points from Grant (1966), Boxall and Stepney (1982), Holt et al. (2001), and Livezey (2009*a*); B) 1910–1979, additional data points from Grant (1966), Reichard (1974), Rogers (1966), Taylor and Forsman (1976), Sharp (1989), Holt et al. (2001), Livezey (2009*a*), and eBird (2019); C) 1910–1999, additional data points from Evens and LeValley (1982), Harrington-Tweit and Mattocks (1985), Sharp (1989), Dark et al. (1998), Hamer et al. (2001), Kelly (2001), Anthony et al. (2006), Livezey (2009*a*), Keane (2017), and eBird (2019); and D) 1910–2018, additional data points from Anthony et al. (2006), Steger et al. (2006), Jennings et al. (2011), Keane (2017), and eBird (2019).

Livezey 2009*a*, *b*), and other vegetation manipulations (Root and Weckstein 1994).

After crossing central North America primarily through Canada (Livezey 2009*a*), the barred owl expanded its range into the Pacific Northwest and south along the west coast, where the first individual was observed in Alberta, Canada in 1912 (Boxall and Stepney 1982), British Columbia, Canada in 1943 (Grant 1966), and in the United States in eastern Washington in 1966 (Rogers 1966), western Washington in 1986 (Sharp 1989), Oregon in 1974 (Taylor and Forsman 1976), northwestern California in 1982 (Evens and LeValley 1982), and along the coast 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; Fig. 1). The western range of the barred owl now overlaps the range of the northern spotted owl (Livezey 2009*a*) and much of the California spotted owl (Keane 2014).

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 to spotted owl surveys (Keane 2017). Keane (2017) reported that the first barred owl in the Sierra Nevada was detected in 1989 in Lassen County. Four more owls were detected between 1989 and 2001 in the northern Sierra Nevada. Between 2002 and 2013, spotted owl researchers recorded incidental sightings of 51 barred owls and 27 hybrids in the Sierra Nevada, the core of the California spotted owl range. Observers using a citizen science program have reported about 60 sightings of barred owls in the Sierra Nevada, as far south as the Greenhorn Mountains in northern Kern County, California in 2017 (eBird 2019). No barred owls have yet been reported in the coastal parts of the California spotted owl range.

To date, few studies have tried to estimate barred owl population size within the range of the spotted owl. In one such case, Kelly et al. (2003) estimated there were 706 barred owl territories in Oregon by 1998, derived from the 2,468 barred owl detections reported in Oregon since the first owl was recorded in 1974. Gutiérrez et al. (2004), however, stated that detection methods that reported cumulative detections may lead to overestimates of barred owl populations. Conversely, Gutiérrez et al. (2004) also stated that most barred owl sightings through the early 2000s were reported incidentally during spotted owl surveys, suggesting that they may be more abundant than estimated.

A modeling framework developed by Zipkin et al. (2017) combined similar detection–non-detection data with count-based data from more recent barred owl-specific surveys (Wiens et al. 2011, Wiens et al., 2014) to estimate population dynamics, abundance, and individual detection probabilities of barred owls in the central Oregon Coast Ranges within historical spotted owl territories (sites). 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.

Wiens et al. (2018) used percent of sites occupied as an index of barred owl numbers as they surveyed 3 spotted owl demographic areas for barred owls in Washington and Oregon in 2015–2016 prior to experimental barred owl removals. They calculated the percentage of 500-ha hexagons (sites) occupied by ≥1 pair of barred owls. They reported in 2015 (pre-treatment) that there were slightly fewer sites occupied by ≥1 barred owl pair in Cle Elum, Washington, than in Coast Ranges, Oregon (54–65% vs. 67–78%, respectively), and similarly fewer individual barred owls/site (1.6–2.2 owls/site vs. 2.6–3.6 owls/site, respectively). Pre-treatment values for Klamath-Union-Myrtle, Oregon (surveyed a year later in 2016), were lower than either of the Washington and Oregon sites, with 39–47% sites occupied by ≥1 pair and 1.2–1.6 owls/site. Reasons for the differences in barred owl densities between Washington, Oregon's Coast Range, and southern Oregon were not identified but could reflect 4 possibilities: variable immigration rates of barred owls; local capacity to support abundant barred owl populations; variation in barred owl saturation across the landscape (i.e., less saturated in southern Oregon relative to Oregon's Coast Range and Washington); or a mixture of the 3 aforementioned possibilities.

The Future of Spotted Owl and Barred Owl Populations

Gutiérrez et al. (2004) outlined and discussed uncertainty regarding future outcomes of the barred owl invasion on spotted owl population viability. They listed 9 potential futures for the northern spotted owl, listed in order of their outcome from most serious to least serious effect, which we reviewed.

Barred owls will replace the northern spotted owl throughout its range (behavioral and competitive dominance hypothesis).— Behaviorally, when spotted and barred owls interact, the barred owl most frequently assumes the dominant role (Van Lanen et al. 2011). Van Lanen et al. (2011) conducted experiments using playback tapes and owl taxidermy mounts for both species. They reported that male barred owls gave more aggressive calls and were more likely to attack the spotted owl mount, whereas male spotted owls were less likely to give aggressive calls or attack the barred owl mount.

Direct confrontations in the field have also been observed. For example, Gutiérrez et al. (2004) reported instances where barred owls have attacked spotted owls and 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 have been 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 a report of a spotted owl pair charging and diving at a barred owl and an aerial clash between a spotted and barred owl (though how the interaction started was not detailed; Jennings et al. 2011).

As the most extreme outcome, barred owls may kill spotted owls, as they are known to depredate other owl species (Graham 2012, Wiens et al. 2014). For example, Graham (2012) found the uneaten remains of 2 unidentified *Strix* species in regurgitated pellets collected during the breeding season near barred owl roost trees or nests. Wiens et al. (2014) found the remains of 2 spotted owls cached beneath fallen logs with wounds consistent with those inflicted by a large avian predator. The researchers were unable to unequivocally determine if they were killed by barred owls because 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, whereby 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. No records have reported that spotted owls might depredate barred owls.

Perhaps because of these aggressive tendencies, barred owls appear to suppress spotted owl responses to conspecific calls, as seen in reduced detection probabilities during surveys when barred owls are present. 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 across their range (Olson et al. 2005; Bailey et al. 2009; Kroll et al. 2010; Dugger et al. 2011, 2016; Sovern et al. 2014). Olson et al. (2005) reported the presence of barred owls was important for modeling detection probability when estimating occupancy of spotted owls, having a negative effect on spotted owl detectability. Gutiérrez et al. (2004), however, stated that even if spotted owls are silent in the presence of barred owls, there does not appear to be a decline in spotted owl recapture rates.

As barred owl populations increase, they can actively displace resident spotted owls from their territories (Sharp 1989, Kelly et al. 2003, Pearson and Livezey 2003). One of the earliest incidents of possible displacement was recorded in Washington by Sharp (1989). In 1985, Sharp (1989) recorded the first barred owls on the east side of the Olympic Peninsula at 2 sites where spotted owls were also located. The following year, no spotted owls were detected, but 2 barred owl pairs were present at those sites, which Sharp (1989) suggested may have been the result of barred owl-mediated displacement of territorial spotted owls.

The presence of barred owls also yields a measurable negative effect on spotted owl territorial colonization and occupancy rates. Five of 6 studies that estimated colonization probabilities reported a negative effect of barred owls on colonization, though it was sometimes weak (Olson et al. 2005; Kroll et al. 2010; Dugger et al. 2011, 2016; Yackulic et al. 2014). Sovern et al. (2014) was the only study that reported no effects of barred owls on colonization rates. Dugger et al. (2016) reported the presence of barred owls resulted in lower local colonization rates at 5 of 11 study areas in the northern spotted owl range. Also, Yackulic et al. (2014) reported that 2 of their top 4 models suggested that spotted owls were less likely to colonize an area that was already occupied by barred owls, whereas barred owls were more likely to colonize areas already occupied by spotted owls.

Dugger et al. (2011) reported that barred owls displaced spotted owls from historical breeding territories during their study in southern Oregon from 1991 to 2006; spotted owl site occupancy was lower where barred owls were detected as compared to sites where barred owls were not detected. Similarly, Kelly et al. (2003) reported that mean annual spotted owl occupancy declined after barred owls were detected within 0.80 km of territory centers in Oregon and Washington from 1987 to 1999, as compared to territories without barred owls. Pearson and Livezey (2003) noted about 20% of 129 spotted owl sites surveyed from 1996 to 2001 were apparently 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 on the eastern slopes of the Cascades in Washington.

The presence of barred owls has also led to an increase in northern spotted owl territorial extinction rates (Olson et al. 2005; Kroll et al. 2010; Dugger et al. 2011, 2016; Sovern et al. 2014; Yackulic et al. 2014). Sovern et al. (2014) stated that the positive relationship between barred owl detections and spotted owl extinction probabilities suggests that spotted owls are being displaced because of competition with barred owls. Modeling of future populations by Yackulic (2017) reported that, without management interventions, the northern spotted owl will be extirpated from most or all of its geographic range; they estimated that it would take from 4 decades to several centuries (median = 88 years) for spotted owls to be driven extinct throughout the Pacific Northwest.

The negative effects of barred owls on spotted owl occupancy appears to worsen as the barred owl invasion continues to advance. For example, at the Tyee study area in Oregon's central coast range, barred owls were first observed aound 1990. Bailey et al. (2009), using data from 2002 and 2003, modeled the co-occurrence of spotted and barred owls using a 2-species occupancy model and concluded there was no evidence that barred owls excluded spotted owls from territories. However, the 2 species co-occurred less often than expected. Ten years later, Yackulic et al. (2014) reported a strong role of intraspecific competition between barred and spotted owls in structuring occupancy dynamics using Tyee data from 1990–2011. Even though their methodologies differed, simulations suggest intraspecific competition had a more substantial effect on equilibrium occupancy values of spotted owls than that of barred owls, especially as the barred owl's invasion advanced. 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. Adding 2 years of data (2012–2013) to the Tyee dataset, Dugger et al. (2016) reported strong evidence that the presence of barred owls was negatively associated with spotted owl colonization rates, and strongly positively associated with spotted owl extinction rates. They reported similarly strong positive associations between the presence of barred owls and territory exinction rates of spotted owls in all 11 study areas.

Spotted owl apparent survival was more strongly and negatively affected by the presence of barred owls as their invasion advanced. Anthony et al. (2006) showed variable effects of barred owls on northern spotted owl apparent survival between 1985 and 2003 in 14 demographic study areas in Washington, Oregon, and California. The strongest negative effects of barred owls were in Olympia and Wenatchee, Washington. Slightly negative effects of barred owls on spotted owls were reported in 1 study area in each of the 3 states (Cle Elem in Washington, H. J. Andrews in Oregon, and northwestern California) and weak to no negative effects were reported in the remaining 9 study areas. Ten years later, using data from 1985–2013, Dugger et al. (2016) reported strong support for declining apparent survival in 8 of 11 demographic study areas across all 3 states.

Studies that examined the effect of barred owls on northern spotted owl fecundity and recruitment have produced mixed results. Three of 6 studies showed no effect of the presence of barred owls on spotted owl fecundity (measured as number of young fledged per female per year; Iverson 2004, Anthony et al. 2006, Dugger et al. 2016). The other 3 studies showed a negative, though not always strong, effect (Olson et al. 2004; Glenn et al. 2010, 2011*b*). However, the presence of barred owls may also affect the detection of spotted owl reproduction. For example, Mangan (2018) reported a strong negative effect of barred owls on the probability of detecting spotted owl reproduction when it was occurring at an occupied site. Additionally, barred owls display demographic superiority, with higher annual survival probabilities, and producing 4.4 times more young than spotted owls over a 3-year period (Wiens et al. 2014).

Glenn et al. (2010) reported that spotted owl recruitment rates were diminished in the presence of barred owls in 4 of 6 study areas. This mixed result may point to other factors influencing fecundity. For instance, Wiens et al. (2014) reported that the number of young fledged by spotted owls increased linearly with increasing distance from the nearest barred owl nest or territory center, and no spotted owl successfully fledged young within 1.5 km of a barred owl nest. When spotted owl young fledged, barred owl detections had no direct relationship with natal or settling locations or dispersal distances (Hollenbeck et al. 2018). Hollenbeck et al. (2018) also reported 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).

Barred owls also appear to have a negative effect on the spotted owl's ability to use high-quality habitats. For example, Davis et al. (2016) modeled habitat suitability in the Tyee density study area in Oregon and reported 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 lower numbers. Pearson and Livezey (2007) reported that late successional reserves (LSRs) in Washington were used more by barred owls than spotted owls for whom they were set aside. They reported 34% more barred owl sites than spotted owl sites in LSRs, whereas there were 33% more spotted owl sites than barred owl sites in non-LSR lands.

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 and may be more lethal to the native species. As such, Lewicki et al. (2015) examined the *Haemoproteus* blood parasite assemblages of barred owls in their native and invasive ranges and in northern spotted owls. They reported 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 barred owls in the West. 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.

Other effects of barred owls on spotted owls include hybridization events that may negatively affect viability of spotted owl populations. The first spotted owl × barred owl hybrids were reported in 1986 (Kelly and Forsman 2004). Since then, ≥ 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 a very low rate of interspecific matings, thereby suggesting that the rate of hybridization will likely not be a serious threat to spotted owl populations. However, they also stated, it is possible that hybridization is more common than reported because hybrid backcrosses are hard to visually identify. Funk et al. (2007) reported that of 12 owls identified as hybrids by plumage in the field, 5 (almost half) were either barred (3) or spotted (2) owls by genetic testing. Hanna et al. (2018) reported no genetic introgression despite hybridization and backcrosses. Forensic genetic investigation shows that the 2 species exhibit extensive evolutionary divergence, and that hybrids are primarily crosses between male spotted owls and female barred owls (Haig et al. 2004). This makes sense when considering that male owls may present females with food during courtship; male barred owls presenting non-mammalian prey to female spotted owls would likely not result in a successful courtship.

Clearly, there is significant evidence that behavioral dominance and competition from barred owls negatively affects spotted owl population viability where the 2 species co-occur. As further evidence of the negative effects of competition, after removal of barred owls in northern California, spotted owl occupancy increased in treated areas while occupancy continued to decline in untreated areas (Diller et al. 2016). The preponderance of evidence suggests that without mitigative efforts, barred owls will eventually drive northern spotted owls to extinction throughout most of their range. By contrast, there is evidence that the spotted owl has not completely succumbed to the barred owl because spotted owl demographic parameters in some study areas have not significantly decreased when subjected to barred owls, and low spotted owl productivity may be underestimated when detection probabilities of spotted owls are diminished in the presence of barred owls.

Barred owls will replace the northern spotted owl in the northern, more mesic areas of its range (moisture-dependent hypothesis).—Given that the most salient examples of barred and spotted owl interactions came from the Pacific Northwest in the 1990s and early 2000s, it was hypothesized that barred owls may be less adapted to drier forests because spotted owl population decline was strongest in the northern, more mesic part of their range and less so in the more xeric forests in northern California at that time (Gutiérrez et al. 2004). The authors recognized, however, that this difference could simply have been due to the earlier phase of colonization in these more northerly areas. This hypothesis also has implications for barred owl invasion throughout the California spotted owl range in drier forests across the Sierra Nevada. Reduced adaptation to drier forests would result in a correspondingly diminished effect of barred owls on spotted owls in drier portions of the spotted owl range (Gutiérrez et al. 2004).

The moisture-dependent hypothesis has merit because barred owls have been reported more often near permanent streams in Washington, Oregon, and California (Herter and Hicks 2000, Wiens et al. 2014, Irwin et al. 2018) and riparian zones (Pearson and Livezey 2003, Singleton et al. 2010) than areas farther away from streams. Moreover, early in the barred owl's expansion into western Washington Cascade Mountains from 1986 to 1989, Hamer et al. (2007) reported that the mean elevation of barred owl territories was lower than that of spotted owls. Additionally, each barred owl territory was adjacent to Baker Lake or along tributaries of the Skagit River, even though the mean distance to nearest perennial stream was not different from random. Herter and Hicks (2000), slightly later in the barred owl expansion in the Washington Cascades in 1991–1993, reported barred owls at their greatest densities on the western side of the range where the environment is wetter, whereas on the drier eastern side, they concentrated along major rivers and streams. Pearson and Livezey (2003), yet a little later in the expansion and just south of the above study site, also reported that occupied barred owl sites were gentler in slope and lower in elevation than those of spotted owls, suggesting that riparian zones and lowland forest were used more by barred owls on the southwestern slopes of the Washington Cascades, and further, that the upland forests were less likely to be occupied by barred owls. However, in Oregon, Wiens et al. (2014) reported that there was broad overlap in habitat use by the 2 species, although, similar to the above studies, the greatest difference in habitat use between the 2 species was barred owls' use of gentler slopes and less reliance on old conifer forest than spotted owls.

Though these data would appear to imply that the 2 species are independently selecting slightly different habitats, particularly when considering elevation, slope, and proximity to streams, it may rather suggest that barred owls are precluding spotted owls from selecting high-quality habitat. For example, Davis et al. (2016), in analyzing the change in spotted owl habitat selection at the Tyee study area in Oregon, reported that the average habitat suitability index for spotted owl sites in 2013 was significantly lower than it was in 1990 when the study began and barred owls had just begun to expand into the study area. This would suggest that spotted owls are using less-quality habitat in the presence of barred owls.

In apparent contradiction to aforementioned and hypothetical differences between barred and spotted owl habitat selection of wet and dry forests, barred owls began to expand into more xeric forests in the eastern Sierra Nevada in 1989 (Keane 2017); although, as noted earlier, barred owl sightings remain low in drier forests when compared to more mesic areas nearer the coast (eBird 2019). Continued expansion of the barred owl into the drier reaches of the Sierra Nevada and southwestern United States should be used as an opportunity to identify key differences in habitat selection between barred and spotted owls; such differences should inform future management action to protect vulnerable populations of spotted owls.

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).—Removal of barred owls was first suggested as a management tool by Gutiérrez et al. (2004), then at later workshops including at a barred owl symposium at the 2018 meeting of The Wildlife Society's Western Section, noting that it would have the added benefit of experimentally 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 spotted 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 population-level productivity. There was also an increase in estimated survival and population growth change, and a decrease in extinction rate. Barred owl removals continued through 2013, resulting in an increased rate of population growth change in treated areas. This was the only experimental removal study area out of 11 across Washington, Oregon, and California, that experienced increasing spotted owl population growth after removals (Dugger et al. 2016).

In 2015, Wiens et al. (2018) began a 5-year barred owl removal study in 3 established study areas: Cle Elem in Washington and Oregon Coast Range and Klamath-Union-Myrtle in Oregon. After removing 883 barred owls from 2015 to 2017, they noted a decline in the probability of use by territorial barred owl pairs in treatment areas. Barred owl local extinction rates were greater in treated areas relative to untreated areas and probabilities of a site being recolonized by a barred owl pair were substantially greater in Cle Elum than in the 2 Oregon study areas. Also, after the second year of removals, more barred owl subadults came in to fill the territories; as they noted, this demonstrated that younger barred owls were available in the surrounding landscapes to quickly fill territory vacancies created by experimental removals.

The question remains if barred owl removals would be successful and feasible throughout the northern spotted owl range. In a limited analysis of one site in the Oregon Coast Range, Bodine and Capaldi (2017) used mathematical modeling to determine if removing barred owls could ultimately save the northern spotted owl population. 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 to preserve the spotted owl population. They determined that, without any action, by 2030 $<$ 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 completely remove them over a 50-year period. To eliminate them in 10 years, it would take an annual removal of over 90% of the barred owl sites. However, their analyses do not include barred owl immigration to the region and, as noted, their study was very limited in scope. Perlman (2017) examined the effects of various barred owl removal rates in 4 existing demographic northern spotted owl study areas using a 2-species individual-based model. She reported that viable, long-term recovery was observed for only 2 of the 4 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 (2017) in that with no removal action taken, the northern spotted owl population would go extinct within 100 years. Baumbusch (2016) investigated the effect of patch size on removals with an individual-based model and reported 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, thereby benefitting spotted owls while decreasing costs. 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, 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 in predicting the effects of barred owl removal as a management tool. Diller et al. (2014) reported the cost for such removals not to be overly burdensome, up to $150/owl in direct costs. Conversely, Livezey (2010) estimated the total cost of the removal study for the Northern Spotted Owl Recovery Plan area to be about $1 million annually ($600,000 direct plus $400,000 indirect costs), breaking down to about $700/owl in the first year and $2,800/owl in subsequent years, if 1,428 barred owls were removed in the first year and 357 each subsequent year. If it is determined that a long-term program is needed, Livezey (2010) suggested that far more than several thousand barred owls would be killed and far more than $1 million would be spent annually.

Ultimately, there are many questions regarding anthropogenic intervention within a natural process of competition and how long any removal program could last (Cornwall 2014, Bodine and Capaldi 2017), given variable immigration rates from either the surrounding areas or areas much farther away. 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 can be achieved at least in certain areas, allowing for coexistence between the species (Buchanan et al. 2007, Pearson and Livezey 2007).

Barred owls will replace northern spotted owls over much of its range, but the spotted owl will persist in refugia (refugia hypothesis).—The expanded range of the barred owl appears to have now completely overlapped that of the northern spotted owl (Wiens et al. 2018). If there are to be refugia for the spotted owl, it might be through partitioning food resources or differentially using specific habitat attributes. Early in the barred owls' expansion in eastern Washington, Singleton et al. (2010) reported that barred owls selected areas with gentle slopes and lower elevations more than expected. Additional early studies also reported similar results: spotted owls used steeper, higher-elevation sites, whereas barred owls used flatter, low-elevation sites, sometimes along streams (Herter and Hicks 2000, Hamer et al. 2007). Pearson and Livezey (2007) reported that elevation and slope were important factors in explaining densities of spotted owls in the southeastern Washington Cascades, 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 detected in 1 LSR, despite the invasion of barred owls in other LSRs, may indicate that local environmental factors such as elevation and slope favor spotted owls over barred owls, and that a natural balance had been achieved in their study area, which allowed the coexistence of these 2 species. Later in the owl's expansion in Oregon, Wiens et al. (2014) reported that spotted owls selected areas with steep slopes with old (> 120-yr-old) conifers, whereas barred owls used flat areas along streams with large patches of hardwoods or conifers (Table 1).

In a recent study, Jenkins et al. (2019) employed light detection and ranging (LIDAR) data to examine vegetation structure used by spotted and barred owls in Oregon's Coast Range and observed that the 2 species may select slightly different habitats. They reported spotted owls selected forests with less canopy cover where trees were tall (>10 m), whereas barred owls were more associated with higher canopy cover regardless of tree height. In addition, when all other covariates were held constant, they reported that spotted owls were more likely to select areas with high coverage of understory vegetation cover 4–8 m tall during the breeding and non-breeding seasons. By contrast, barred owls were more likely to select areas with low amounts of understory vegetation cover 4–8 m tall during the breeding season but selected for higher understory cover in the nonbreeding season. They also reported that slope had nearly equal but opposite effects on the relative probability of habitat selection for both species; barred owl relative probability of use was 2.2 times greater than spotted owl for slopes < 9°, whereas spotted owl probability of use was 2.3 times greater than barred owl for slopes > 36°, similar to earlier studies showing differential use of steeper terrains by spotted owls.

If viable populations of northern spotted owls exist in equilibrium with barred owls, these unique situations need to be further investigated to identify those resources and habitat attributes differentially selected by the 2 species; such findings would greatly inform future management actions. However, these few populations in apparent equilibrium (Pearson and Livezey 2007) may be subject to an extinction debt, destined to be paid by the continued expansion and growing population of barred owls.

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).—potted 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 flying squirrels (*Glaucomys* spp.). Although more than half of barred owl diets depended on larger mammals such as flying squirrels, they also included a greater percentage of smaller mammals (e.g., shrews [*Sorex* spp.] and moles [*Scapanus* spp. and *Neurotrichus gibbsii*]), birds, amphibians, and arthropods (Table 2).

Barred owl diets vary between regions, demonstrating a broad dietary breadth. Graham (2012) examined barred owl pellets from 3 study areas: Olympic National Forest and the eastern slope of the Cascades in Washington, and the Central Coast Range in Oregon. He reported that their diet was considerably different between the 2 western mountain range study areas and the eastern Cascade Range, which is considerably drier and hotter (Table 2). In the eastern mountains, barred owls did not depend as much on mammals, which comprised only 26.5% of their diet, but instead relied more on arthropods (47.0%) and amphibians and reptiles (22.9%). These studies may not reflect the full range of spotted or barred owl diets; Livezey et al. (2008) reported 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 taken by spotted and barred owls can differ in activity periods, behavior, and habitat associations. In western Washington, Hamer et al. (2001) reported that spotted owls most often predated nocturnal and arboreal species, and

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 western Oregon, USA, 2007–2009. Forest types are expressed as the mean percentage of total foraging, roosting, or random locations. Sample sizes (number of individual owls or random points) are in parentheses. From Wiens et al. (2014).

	Spotted owl				Barred owl				Random	
	Foraging ($n = 25$)		Roosting ($n = 16$)		Foraging ($n = 26$)		Roosting ($n = 22$)		($n = 11{,}947$)	
Environmental condition	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	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 or 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 (number/ha)	17.0	0.6	20.1	0.4	15.4	0.7	16.4	0.3	10.9	0.1
Canopy cover of hardwood (%)	20.7	0.7	19.7	0.2	19.0	0.8	18.5	0.2	19.2	0.1
Basal area of hardwoods (m^2/ha)	5.4	0.2	5.0	0.1	4.7	0.2	4.6	0.1	5.0	0.1
Slope (degrees)	46.6	1.3	50.1	0.6	39.7	1.7	41.4	0.6	44.3	0.2
Distance to high contrast edge (m)	470.3	49.3	478.3	16.3	500.0	56.5	535.4	13.8	401.1	4.9
Distance to stream (m)	387.3	18.8	398.2	11.6	360.4	37.9	374.1	10.7	453.1	3.2
Distance to nest (m)	2,879.1	428.5	2,868.1	159.3	963.0	71.1	831.3	34.0	3,674.0	42.7

Table 2. Select barred owl and spotted owl prey items found in regurgitated pellets from 3 studies in Washington and Oregon, USA. Percent of total number of individual prey items identified in owl pellets and prey items are listed, with number of territories sampled (Wiens et al. 2014) or number of family areas sampled (Graham 2012) in parentheses. No sample size was reported for western Cascades (Hamer et al. 2001).

	Spotted owl		Barred owl			
Prey	**Western Cascades, WA[a]**	**Central Coast Range, OR[b] ($n = 16$)**	**Western Cascades, WA[a]**	**Central Coast Range, OR[b] ($n = 25$)**	**Central Coast Range, OR[c] ($n = 25$)**	**Olympic National Park, WA[c] ($n = 20$)**	**Eastern Cascades, WA[c] ($n = 9$)**
Mammals	96.2	95.7	76.1	66.0	64.3	71.7	26.5
Moles, shrews	4.0	2.7	23.8	31.7	32.2	34.1	5.1
Lagomorphs	6.0	3.4	8.3	2.5	1.4	0.5	1.2
Flying squirrel	50.7	37.8	20.0	11.6	10.3	15.5	12.2
Douglas's squirrel (*Tamiasciurus douglasii*)	1.7	0.8	8.3	2.0	2.0	2.1	1.5
North American Deermouse (*Peromyscus maniculatus*)	20.6	17.3	6.8	3.5	4.0	3.7	1.5
Woodrats (*Neotoma* spp.)	4.4	8.1	0.0	1.5	1.3	0.0	0.3
Red tree vole	0.0	14.7	0.0	3.4	3.9	0.0	0.0
Birds	2.8	3.1	11.0	2.8	2.7	6.4	3.6
Fish	0.0	0.0	2.6	0.2	0.2	0.5	0.0
Amphibians and reptiles	0.0	0.1	5.7	9.1	11.1	7.5	22.9
Arthropods	1.0	1.0	3.8	12.5	15.0	10.7	47.0
Gastropods	0.0	0.2	0.8	6.9	6.8	3.2	0.0

[a] Hamer et al. (2001).
[b] Wiens et al. (2014).
[c] Graham (2012).

those inhabiting forests and talus slopes. By contrast, barred owls predated more diurnal and terrestrial species, and those in forests, meadows, and riparian zones. Barred owls did not predate any food items associated with talus slopes.

Even with the addition of a competitor, the diet of the spotted owl in the Oregon Coast Range detailed by Wiens et al. (2014) in 2007–2009 (after the arrival of barred owls) is remarkably similar to that reported for spotted owls before barred owls arrived, as studied by Forsman et al. (1984) between 1970 to 1980. Forsman et al. (1984) reported for all years combined that 89.2% of the prey items were mammals, with flying squirrels as the primary prey at 35.2%. This comparison suggests that the spotted owl is not able to change its diet in the face of competition by a congeneric species.

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 affect the food web and associated ecological processes in unforeseen ways, thereby affecting the ability of the ecosystem to support populations of 2 similar predators (Holm et al. 2016). Holm et al. (2016) reported that potential effects of adding barred owls to the ecosystem on the food web included restructuring of prey communities, changes in prey behavior, increased predation pressure for shared primary prey species (such as flying squirrels, red tree voles [*Arborimus longicaudus*], and lagomorphs), and declines in secondary prey species. Because spotted owls are prey specialists, these changes may have a greater adverse effect on spotted owls, which rely on mammalian prey when compared to the generalist barred owl.

Barred owls will replace spotted owls only where weather and habitat change have placed spotted owls at a competitive disadvantage (synergistic effects hypothesis).—Climate and weather can have a variable effect on spotted owl demography. For instance, Glenn et al. (2010) when analyzing 6 demographic study areas in Washington and Oregon, reported that the amount of annual variation in population growth change influenced by climate was highly varied across their study sites, explaining from 3% to 85% of the model's variation. By contrast, Franklin et al. (2000) reported that climate explained most of the temporal variation in life-history traits in a smaller study in northwest California.

Apparent survival for spotted owls has been reported to be negatively affected by increased precipitation during the spring nesting season (Mar–Apr; Franklin et al. 2000) but positively affected by wetter than normal growing seasons (May–Oct; Glenn et al. 2010, 2011*a*). Higher spring (Mar–Apr) temperatures were also reported to positively affect spotted owl survival (Franklin et al. 2000). During the nesting season (Mar–Jun), an increase in numbers of winter storms was reported to negatively affect survival at 1 study site (Glenn et al. 2010). In a meta-analysis of their 6 study sites, Glenn et al. (2011*a*) reported that climate accounted for only a slight amount of temporal variation in survival and was associated with the Southern Oscillation and Pacific Decadal Oscillation cycles; survival was higher when the Southern Oscillation was in the La Niña phase and the previous year's Pacific Decadal Oscillation was cool and wet.

Reported effects of climate on spotted owl fecundity are variable. Dugger et al. (2016), studying 11 demographic study areas from Washington to California, reported that top fecundity models contained climate covariates at 8 of 11 study areas, but the best covariate and the direction of those correlations varied between study areas. For example, in their study, in 3 areas there was a positive effect of mean monthly minimum temperature during the early nesting season, whereas in 2 areas the effect was negative. For precipitation during early nesting periods, the effect was negative in 1 area and positive in a second area. Not surprisingly given this variability, when Dugger et al. (2016) ran a meta-analysis for fecundity using the entire dataset, no models with climate variables were reported to be competitive. By contrast, in a smaller study in the Siskiyou National Forest of southwestern Oregon, Zabel et al. (1996) reported that fecundity was strongly negatively correlated with total precipitation during the nesting season. They reported that the index of precipitation explained about 85% of the variance in fecundity. Similarly, in the south Cascades and Siskiyou Mountains in southern Oregon, Wagner et al. (1996) reported fecundity to be negatively correlated with precipitation from the previous September to April.

Reproductive output for spotted owls was negatively associated with increased precipitation and colder temperatures during the nesting period (Franklin et al. 2000; Glenn et al. 2011*a*, *b*). It was also negatively associated with total winter snowfall in 1 study area (Glenn et al. 2011*b*). Glenn et al. (2010) reported spotted owl recruitment was positively associated with wetter than normal growing seasons (May–Oct). Similarly, in northwestern California Franklin et al. (2000) reported recruitment to be positively correlated with increased precipitation during early spring; however, they reported recruitment was negatively associated with increased days of winter precipitation.

By contrast to the above spotted owl research, few studies have examined the effects of climate on barred owls to make comparisons. However, if some of the above effects reflect spotted owl prey dynamics (activity and populations; Franklin et al. 2000; Glenn et al. 2010, 2011*a*, *b*) or decrease owl hunting efficiency (Franklin et al. 2000) as some have hypothesized, then the effects would likely be less severe for barred owls considering their expansive dietary breadth relative to spotted owls.

Franklin et al. (2000) suggested that extreme climate conditions during the early nesting period (Mar–Apr) might exacerbate the energetic stress on an individual spotted owl by decreasing its time to starvation. They estimated that a spotted owl would reach starvation level within an estimated 8 days at maintenance metabolic rates. This may create greater stress on the smaller spotted owl, relative to the larger barred owl (Gutiérrez et al. 2007).

Climate projections for much of western North America suggest drier weather punctuated by periods of intense precipitation resulting in more severe wildfires (Wan et al. 2019), which could further affect spotted owl populations. Research has shown both negative and positive effects of wildfire, timber harvest, and fuels treatments on spotted owl populations (Ganey et al. 2017). For example, Seamans and Gutiérrez (2007), studying California spotted owls from 1990 to 2004 in the Sierra Nevada, reported that owl populations were negatively affected by alteration of their habitat, either by stand-replacing fire or timber harvest. In particular, they reported that the alteration of ≥20 ha of mature coniferous forest in territories negatively affected population growth of California spotted owls. Also, for territories in which ≥20 ha of mature coniferous forest was altered, California spotted owls experienced a 2.5% decline in occupancy probability. In the northern Sierra Nevada in eastern California, Gallagher (2010) assessed home range sizes of 8 California spotted owls in areas altered by recent fuels treatments, and reported that home range area increased, a sign of declining habitat quality, as the total area of fuels treatments within the home range increased. These fuels treatments, called defensible fire protection zones (DFPZs), reduced canopy cover, tree density, and ladder fuels. The use of fuels treatments varied widely between owls, with 4 owls not using the treated areas at all (7–18% of their home ranges), to 1 owl spending 53% of its time within fuels treatments while 28% of its home range consisted of treatments. At the scale of the entire study area, owl use of DPFZs was less than expected by random chance, thus suggesting that spotted owls avoided fuels-treated areas.

Bond et al. (2009) reported that California spotted owls used all severities of burned forest for nesting, roosting, and foraging during the breeding season 4 years after a large forest fire. Also, spotted owls selected burned areas for foraging over unburned forest, with the greatest use of high-severity burned areas. Conversely, Jones et al. (2016) reported an overwhelming negative effect of high-severity fire on spotted owls, where probability of extinction within several California spotted owl territories was 7 times higher after a large fire than before the fire. Contrasting results and inferences surrounding the response of California spotted owls to fire has resulted in recent accusations of agenda-driven science (Peery et al. 2019).

Franklin et al. (2000), using data collected between 1985 and 1994 from northwestern California before barred owls had severely affected the area, reported that a mosaic of older forest interspersed with other vegetation types promoted high northern spotted owl fitness. Results from Franklin et al. (2000) suggest that spotted owls use mature forest to roost, nest, and hunt and use forest edges between older stands and younger sapling or brushy stands for foraging where prey may be more abundant (Zabel et al. 1995).

In general, spotted owls are sensitive to the loss of large and mature forest in territory centers where they roost and nest and are sensitive to fuels treatments that reduce canopy cover and ladder fuels. With climate change leading to a possible increase in fires, fuels treatments become an important component of restoring fire resiliency to western forests and raise serious challenges for forest and wildlife managers regarding spotted owl management. Specifically, given that fuels treatments can reduce spotted owl fitness, thereby making populations more vulnerable to barred owl-mediated extinction, managers might want to consider strategically integrating barred owl removals into forest planning and restoration.

Barred owls will replace northern spotted owls in some vegetation communities but not in others (habitat hypothesis based on structural elements of forest, which confer a maneuverability advantage to the smaller spotted owl).—A few smaller studies have examined the owls' use of forest understory components. In northern California, Weisel (2015) examined the owls' use of understory components within redwood (*Sequoia sempervirens*) forests and reported that habitat used for foraging by both species was positively influenced by the percent of understory vegetation, though barred owls were more likely than spotted owls to select foraging habitat with a greater percentage of understory vegetation. Both owls were positively influenced by the relative amount or percent of hardwoods and the density of hardwoods by basal area, though barred owls selected foraging habitat with a greater percentage of hardwoods than spotted owls up to a certain volume when the author suggests that the stand becomes too dense to support successful barred owl foraging. Similarly, Irwin et al. (2018) suggested 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.

By contrast, Jenkins et al. (2019) reported that barred owls in the breeding season selected areas with low coverage of understory vegetation 4–8 m tall, whereas spotted owls were more likely to select areas with higher coverage of that vegetation type; however, in the non-breeding season in areas of tall canopy (17.3 m), both spotted and barred owls selected areas with higher amounts of understory vegetation 4–8 m tall. This would support the hypothesis that spotted owls regularly select habitat with denser vegetation compared to barred owls, at least during the breeding season.

From 1982 to 2000, Pearson and Livezey (2003) surveyed for spotted and barred owls in the southwestern Washington Cascade Mountains and reported that the mean age of forest stands at site centers was significantly greater for spotted owls than for barred owls (254.7 yr vs. 228.3 yr, respectively). This study was early in the barred owl expansion in southwestern Washington (there were no barred owls detected in 1982, the first year of the study); by 2000, about 30% of all *Strix* species detected were barred owls. Also, Hamer et al. (2007) reported that, early in the barred owl's expansion, 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 enlarge their home range to increase amount of old forest in their territory. This was only slightly true for barred owls. In Washington, Herter and Hicks (2000) reported that spotted owl territories contained more mature coniferous forests than barred owl territories. Similarly, in the eastern Washington Cascades, Irwin et al. (2004) reported that abandoned spotted owl territories had greater amounts of forest dominated by pole-sized (13–19 cm dbh) trees, suggesting that spotted owls used habitat with larger trees. Conversely, in Oregon, Wiens et al. (2014) reported that both species used patches of old (>120 yr) coniferous forest in proportions 2 to 3 times greater than available in the study area (Table 1).

Barred owls select more complex forest over more open habitat throughout their lifecycle. For example, Singleton (2015) compared the intensity of barred owl use of 3 land cover types, and reported intensity of use during the breeding season was higher in complex-structure grand fir (*Abies grandis*) compared to the more open, recently disturbed ponderosa pine (*Pinus ponderosa*) and more simple-structured Douglas-fir (*Pseudotsuga menziesii*) with intermediate amounts of upper-layer canopy cover. The most selected forest type, grand fir, had taller trees with more diverse tree heights, more total trees per hectare, higher tree canopy, and open ground cover < 0.6 m. During the non-breeding season, barred owls used habitat with gentler slopes, greater tree species diversity, and more trees per hectare of any size.

The few studies examining variation in use of specific habitat attributes between barred and spotted owls may suggest some difference in foraging and nesting habitats. However, the overwhelming majority of evidence demonstrates that habitat use and selection broadly overlaps between the species, so much so that contemporary habitat differentiation and specialization is unlikely. If the northern spotted owl does not go extinct, competition between the species may serve as an evolutionary selective force resulting in character displacement between the species, and subsequent niche differentiation (Diamond et al. 1989). However, current population declines of spotted owls strongly suggests that character displacement will not take place prior to extinction of the northern spotted owl.

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).—Though barred owl expansion continues to diminish spotted owl populations where the species overlap, spotted owls may be able to persist in areas with higher-quality spotted owl habitat. Using data from 1985 through 2013, range-wide estimates of population change for spotted owl populations showed declines from 1.2% to 8.4% per year depending on the study area, with an estimated range-wide decline of 3.8% per year from 1985 to 2013 (Dugger et al. 2016). Barred owl presence was associated with increased spotted owl territorial extinction rates in all areas; however, a greater amount of spotted owl habitat generally decreased those rates, suggesting that quality habitat may buffer spotted owl populations from the deleterious effects of barred owls.

As barred owl populations increase, they have been reported to form new territories within spotted owl

Table 3. Comparison of home range sizes ($\bar{x} \pm$ SE ha) for northern spotted owls and barred owls in Washington, Oregon, and northern California, USA. Hamer et al. (2007) estimates were calculated using 95% adaptive kernel method, all others used 95% fixed kernel method.

			All		**Females**		**Males**	
Study	**Area**	**Season**	**Spotted owl**	**Barred owl**	**Spotted owl**	**Barred owl**	**Spotted owl**	**Barred owl**
Hamer et al. (2007)	Baker Lake, WA	Annual	2,659 ± 626	781 ± 216	3,517 ± 1,091	527 ± 51	1,706 ± 392	1,184 ± 545
		Summer	1,505 ± 288	299 ± 30	1,783 ± 464	299 ± 33	1,199 ± 321	300 ± 58
		Winter	2,920 ± 868	950 ± 268	2,954 ± 857	579 ± 75	2,875 ± 1,714	1,488 ± 631
Wiens (2012)	Central Cascades, OR	Annual	2,813 ± 290	879 ± 110	3,165 ± 490	737 ± 77	2,507 ± 332	1,015 ± 201
		Breeding	1,620 ± 193	556 ± 41	1,508 ± 288	487 ± 57	1,712 ± 265	614 ± 57
		Nonbreeding	2,688 ± 273	1,028 ± 139	3,008 ± 450	874 ± 114	2,351 ± 292	1,168 ± 243
Schilling et al. (2013)	Klamath Mountains, OR	Annual	576 ± 75		511		630	
		Breeding	491 ± 97					
		Nonbreeding	469 ± 59					
Weisel (2015)	North Coast Range, CA	Breeding	391 ± 79	303 ± 37				
		Nonbreeding	560 ± 159	442 ± 97				

territories without displacing spotted owls (Wiens et al. 2014). When barred owls establish territories inside spotted owl territories, some barred owl territories may be contained entirely within spotted owl territories because the estimated size of spotted owl territories can be > 6 times the size of barred owl territories (Table 3; Hamer et al. 2007, Wiens 2012, Wiens et al. 2014). Wiens et al. (2014) reported that each individual spotted owl in their study area shared a portion of its home range, usually foraging areas, with 0–8 barred owls in adjacent territories ($\bar{x} = 2.4$ barred owls/spotted owl territory). Similarly, in an earlier study, Dugger et al. (2011) reported that some spotted owl pairs retained territories and continued to survive and successfully reproduce on territories where barred owls were detected. However, spotted owls are less likely to use an area if it was within or near a barred owl core area (Wiens et al. 2014), and as we noted earlier, spotted owl reproductive and demographic parameters are negatively affected by the proximity or presence of barred owls.

Although quality habitat may buffer spotted owls from the negative effects of barred owls, quality habitat may simply prolong the inevitable local extinction of spotted owl populations. Nonetheless, without management plans that promote barred owl removals, management prescriptions that promote quality spotted owl habitat may be the best option for sustaining spotted owl populations in the short-term and, possibly, over longer time scales as well (U.S. Fish and Wildlife Service 2011).

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).—Barred owl populations in the north, where the owls were first observed, may have stabilized at this time, but no studies have estimated the barred owl population size over time to compare rates of barred owl population change. However, it would appear that barred owls continue to increase across the Pacific Northwest given that Dugger et al. (2016) reported that the proportion of spotted owl territories with barred owls continue to increase for each of 11 study areas in Washington, Oregon, and California.

Conversely, northern spotted owl populations continue to decline across its range. Dugger et al. (2016) reported that the rate of population change for northern spotted owls was < 1.0 (range = 0.878–0.988) in all study areas with the exception of the Green Diamond barred owl removal experimental area in northern California (1.030). Given that barred owls occur at higher densities than spotted owls, hypothetical natural population declines of barred owls may not result in the positive population growth of spotted owls necessary to sustain viable populations.

DISCUSSION

In reviewing alternate future outcomes for spotted and barred owl populations (Gutiérrez 2004) and associated evidence, we concluded that the future for northern spotted owls is bleak. Comparatively, barred owls are larger (Gutiérrez 2007); behaviorally and competitively dominant (Van Lanen et al. 2011); negatively affect the survival, productivity, recruitment, and population viability of spotted owls (Dugger et al. 2016, Mangan 2018); increase spotted owl extinction rates (Dugger et al. 2016); and display demographic superiority to spotted owls (Wiens et al. 2014).

The rapid expansion of barred owls across the Pacific Northwest and, more recently, through the Sierra Nevada has motivated conservationists, researchers, and managers to assemble the local and regional management plans necessary to mitigate the harmful effects of barred owls on spotted owls. With the start of an experimental 5-year plan to lethally remove barred owls from demographic study areas (Diller et al. 2014, 2016; Wiens et al. 2017, Wiens et al., 2018), there is evidence that removals can increase population growth of spotted owls in at least some areas. As noted earlier, evidence also suggests that quality habitat may buffer spotted owls from the negative influences of barred owls (Dugger et al. 2016) and that spotted owls may have slight differences in use of forests and terrain, such as denser understory and steeper terrains, to carve out refugia (Jenkins et al. 2019). Thus, strategic removals coupled with management prescriptions that promote quality spotted owl habitat may represent the 2-pronged strategy necessary to save the species, or at least slow population decline until new alternatives can be identified.

More research into barred owl natural history within its expanded range is needed. Peery et al. (2018) outlined categories of barred owl research for California, many of which are also applicable to barred owl populations in Washington and Oregon. These research objectives include 1) improve our understanding of barred owl distribution, habitat associations, density and expansion; 2) initiate removal experiments in spotted owl areas with low densities of barred owls; 3) understand the dispersal ecology and recruitment of juvenile barred owls; 4) model proposed barred owl removal strategies and potential spotted owl refugia locations; and 5) understand the broader effects of barred owl foraging on ecological processes. Based on this review, to this list we would add research that directly compares the response of barred and spotted owls to habitat modifications (e.g., fuels treatments) including interactive effects between the species. In addition, more research is needed to determine the temporal and spatial dynamics of barred owl recovery following removal efforts. This information will help create informed management plans given variable levels of barred owl saturation throughout western North America.

Lastly, we suggest managers use this review and the associated annotated bibliography (Appendix S1, available online in Supporting Information) to develop and evaluate the potential of large-scale barred owl removal plans. The burgeoning availability of platforms to develop individual-based models provide opportunities for managers to test and refine removal plans prior to implementation (Baumbusch 2016). After refinement and implementation, continued monitoring programs will provide new information, such as barred owl recovery rates, that can be used to further refine removal plans, thereby creating an adaptive management loop for barred owl removal and spotted owl recovery.

MANAGEMENT IMPLICATIONS

We agree with Holm et al. (2016) that removal of barred owls from high-quality habitat with dense populations of spotted owls would benefit spotted owls, dependent on the results of current removal studies (U.S. Fish and Wildlife Service 2013, Diller et al. 2016, Wiens et al. 2018). Although these management actions may provide protection for spotted owls in local, high-quality habitats, we affirm the need to consider removal efforts at the landscape scale in collaboration with public and private entities. Specifically, private timber companies and Tribal governments could be incentivized to initiate barred owl removal programs on their respective properties. After any removal efforts, we recommend rigorous monitoring programs to determine the rate at which barred owl recovery occurs. Long-term post-removal recovery rates of barred owls are largely unknown but represent a necessary facet of their ecology to inform management planning. Additionally, coupling barred owl removal with management action that promotes quality spotted owl habitat may reflect the 2-pronged approach necessary to ensure the persistence of the northern spotted owl into the twenty-second century.

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Summarizing statements for Online Table of Contents:

We reviewed evidence for future outcomes of northern spotted owl populations given continuing expansion of barred owls across western North America, and our results suggest that without aggressive management action, the future for northern spotted owls is bleak. Specifically, we suggest managers consider a 2-pronged management approach consisting of barred owl removal in quality habitat with dense populations of spotted owls and management strategies that promote quality spotted owl habitat.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.