

The invasion of barred owls and its potential effect on the spotted owl: a conservation conundrum

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Abstract The spotted owl (*Strix occidentalis*) is a threatened species in many areas of its western North American range. Concomitant with its decline has been a rapid invasion of its range and habitat by barred owls (*Strix varia*), a native species that was restricted, until relatively recently, to eastern North America. We assess the theoretical potential for negative interactions between these two owls by examining size dimorphism and ecological relationships within various owl assemblages throughout the world. We then review the anecdotal, natural history, modeling, and experimental evidence that suggest barred owls may negatively affect spotted owls with at least a potential for the competitive

exclusion of spotted owls by barred owls throughout all or part of the former's range. While it is widely accepted that barred owls are either causing or exacerbating declines of spotted owl populations, there are confounding factors, such as habitat loss and bad weather that also may contribute to declines of spotted owls. Both theory and empirical information suggest that barred owls are likely to have negative effects on spotted owl range and density, but the degree of the impact is not predictable. There is a conservation conundrum here, in that the barred owl is a native species that has expanded its range westwards, either naturally or with a degree of human facilitation, and now constitutes a major threat to the viability of another native species, the threatened spotted owl. We propose that only through carefully designed experiments involving removal of barred owls will we be able to determine if recent declines in spotted owl populations are caused by barred owls or by other factors. It is rare in conservation science that replicate study areas exist for which we also have long-standing demographic information, as is the case with the spotted owl. Removal experiments would take advantage of the wealth of data on spotted owls, and allow ecologists to assess formally the impacts of an invasive species on a threatened species, as well as to suggest mitigation measures.

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Introduction

The historic range of the barred owl (*Strix varia*), prior to the mid 1900's, was confined to eastern North America, from southeastern Canada south to western Mexico (Rignall 1973; Mazur and James 2000). Subsequently, the barred owl has invaded the range of the northern spotted owl (*Strix occidentalis caurina*) in western North America. This range expansion has significant conservation implications because the barred owl was identified as a potential threat to the northern spotted owl when it was initially listed as a threatened species (USDI 1990, pp. 26, 191). Yet many facets of the barred owl's invasion are uncertain including the degree to which it poses a threat to the spotted owl. Thus, the invasion of barred owls presents a conundrum for conservation action because it is a native species, but it is expanding beyond its historic range and may have the potential to threaten the viability of the threatened northern spotted owl, also a native species. Moreover, a failure to address this invasion has significant implication for conservation of old growth forests and other species. Therefore, in this paper we provide a framework based on predictions from theory and empirical data to begin evaluating the ecological effects of barred owls on spotted owls (Parker et al. 1999). Through this framework, we provide suggestions to help resolve this and similar conundrums.

Range expansion of barred owls

The barred owl has been expanding its range westward in North America for more than 80 years, and now is entirely sympatric with the northern spotted owl (Gutiérrez et al. 2004; Anthony et al. 2006). In less than 10 years the barred owl expanded its range from western Washington to northern California (Taylor and Forsman 1976; Evens and LeValley 1982). In

addition, they have invaded the range of the California spotted owl (*Strix occidentalis occidentalis*) in the Sierra Nevada of eastern California, USA (Seamans et al. 2004). It is not clear if this expansion is natural or human influenced (Dark et al. 1998, Gutiérrez et al. 2004). Regardless, the barred owl now co-occupies essentially all of the range of the northern spotted owl, and to a lesser degree, the Sierra Nevada range of the California spotted owl. Within this expanded range, barred owls continue to move into new areas, but their rate of spread within habitats is variable (Dark et al. 1998). However, there have been no systematic surveys of barred owls within the ranges of the northern and California spotted owls, so it is not clear if observations on their relative rate of spread are reliable.

Evaluating the potential negative impact of barred owls on spotted owls

Theoretical evidence

Body size and coexistence patterns in sympatric owl species

We examined patterns of body size in coexisting owl species to identify characteristics of species that commonly co-occur syntopically to better evaluate the potential for coexistence of barred and spotted owls in their new area of sympatry in northwestern North America. We view these inferences as preliminary because the published data on syntopic owls are variable in depth and quality.

With exceptions detailed below, most congeneric owls are allopatric in range. Some congeneric owls that are sympatric in range often segregate by habitat, and therefore, are not syntopic (del Hoyo et al. 1999). For example, the western screech-owl (*Megascops kennicotti*) occupies more open habitats than the sympatric whiskered screech-owl (*M. trichopsis*) in Arizona and the eastern screech-owl (*M. asio*) in Texas (Marshall 1957; Gehlbach 1995). The western screech-owl is generally segregated from the flammulated owl (*O. flammeolus*) by its use of

woodlands at lower elevations (McCallum 1994). In most cases, owls that coexist within the same habitat belong to different genera, and coexistence is apparently promoted by interspecific differences in behavior, such as hunting modes and prey selection (Mikkola 1983; Jaksic and Carothers 1985; Johnsgard 1988). Owls share with diurnal raptors conspicuous differences in body size among coexisting species, size differences that co-vary with prey choice and perhaps also with hunting mode. Size differences among owl species are further accentuated by gender-based size differences within species. Reverse sexual size dimorphism is typical of owls, as it is in diurnal raptors, with females larger than males in body size (Earhart and Johnson 1970).

Most coexisting owl assemblages in the world contain either three ($n = 9$ assemblages) or four species ($n = 8$ assemblages; Appendix 1). However, five- and six-species assemblages are found in African savannah and neotropical rainforest, respectively, and indicate that owl species richness mirrors the general trends of avian species richness, each conspicuously high in both neotropical forests and African savannahs relative to temperate woodlands. We present logarithms of body mass of coexisting owl species in Fig. 1, in which male and female body sizes are averaged. Conspicuous size segregation occurs at all sites except the Australian site (U; see Appendix 1), which lacks small owls and also differs in that the larger *Ninox* species do not show reversed sexual dimorphism. For these reasons, we omit the Australian site from the following analysis.

Overall, size ratios ($\log A/\log B$, where A and B are body sizes [masses] of adjacent species in a size series) tend to become smaller in assemblages with larger numbers of coexisting species: 3-species = 0.485; 4-species = 0.398; 5-species = 0.332; 6-species = 0.240. However, size ratios are not significantly different between the smaller and larger adjacent species pairs in either 3- or 4-species assemblages, and mean size ratios do not differ significantly between 3- (0.485 ± 0.184 SD; $n = 18$) and 4-species assemblages (0.398 ± 0.177 SD; $n = 24$) by t -tests ($df = 34$, $t = 1.446$, $0.2 > P > 0.1$). Thus, in general, adjacent species in a size series differ by a factor of 3.05 in body mass in 3-species assemblages of

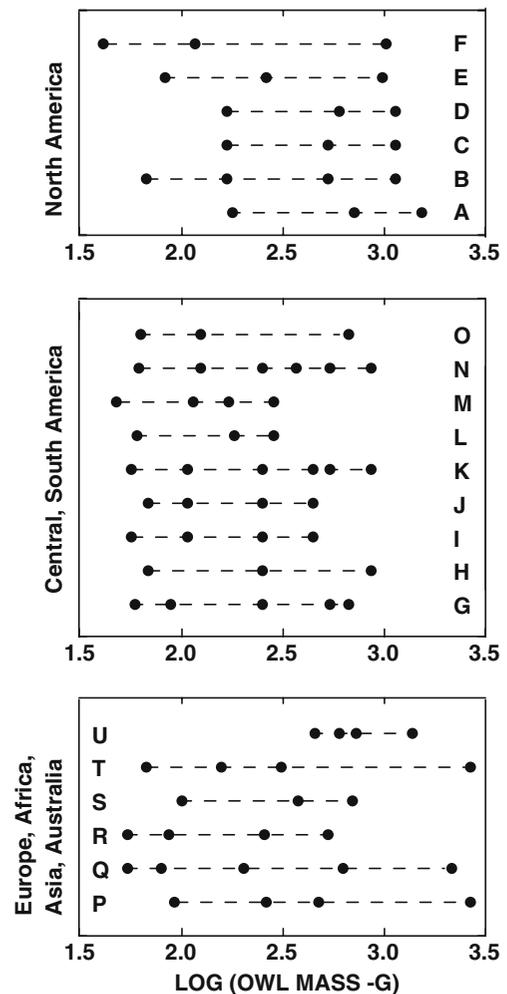


Fig. 1 Sets of coexisting owl species on six continents, illustrating size segregation of coexisting species. More detailed site descriptions and definitions of codes A to U are in Appendix 1

coexisting owls, and by a factor of 2.50 in 4-species assemblages.

Most of these sets of coexisting species consist of species in different genera (as well as different body sizes); this is the case with the six species at Cocha Cashu, Peru (Site N; Terborgh et al. 1990). However, sites M (Graves 1985) and Q (Voous 1966) support two *Otus* species of different sizes, and the latter site also supports two *Bubo* species of different sizes. Roberts (1991; site T) reports that as many as three *Otus* species may be found together in the Murree Hills of Pakistan during the summer (*O. spilocephalus*, *O. bakkamoena*, *O. sunia*). Two species of *Strix* occur at sites G

(Schaldach 1963), I (Howell 1999), J (Land 1963) and K (Enriquez-Rocha and Rangel-Salazar 2001). Indeed, *Ciccaba virgata* and *C. nigrolineata* coexist throughout a broad range of neotropical forest (e.g., SE Nicaragua; M. L. Cody, unpublished data). Thus, although most congeneric species are segregated by geographic range or by habitats, in some cases congeneric species coexist at the same site and contribute to local α -diversity. However, coexisting congeneric species display a degree of size divergence comparable to that of coexisting species in different genera.

Sympatry and coexistence in the genus Strix/Ciccaba

König et al. (1999) list 21 species in the genus *Strix/Ciccaba* complex (Note: we use the American Ornithologists' Union Checklist as the authority for nomenclature of North and South American owl species) distributed throughout Eurasia, Africa, North and South America. Most are medium to large owls, but body size varies from 175 g (male *S. butleri*, Arabian Peninsula) to 1280 g (female *S. bartelsi*; Sumatra); female *Strix* exceed male mass by a factor averaging 1.28, with a tendency for this factor to increase with absolute size. We examined a few continental examples of sympatry with respect to differences in habitat use and body size in coexisting *Strix/Ciccaba*.

In Europe and western Asia, three *Strix* species occur which are broadly segregated by latitude of breeding range, with *S. nebulosa* in the north, *S. aluco* in the south and *S. uralensis* in between (del Hoyo et al. 1999). All three species are sympatric in central Sweden and southern Finland, but there are general habitat differences that correspond to differences in geographic ranges, with *S. nebulosa* in open conifer forests, *S. uralensis* in deciduous to mixed conifer forests, and *S. aluco* in deciduous woodlands and into park- and farm-lands. All feed mainly on small mammals. Mean body sizes (average of male and female from Sweden and Finland) are 390–785–1080 g for *aluco*, *uralensis*, and *nebulosa*, respectively. Thus, body size ratios are 2.01 and 1.38, the latter number (for larger species pairs) considerably smaller than the norm for coexisting owl species (Mikkola 1983; Vrezec 2003).

The tawny owl (*Strix aluco*) has expanded its breeding range north since 1875 (Mikkola 1983). In Finland, territory sizes of *S. aluco* are much smaller (ca. 50–100 ha) than those of *S. uralensis* (ca. 450 ha); where the two occur in similar habitat, nests are generally 2–4 km apart (Lammin-Soila and Uusivuori 1975 in Mikkola 1983). These two species are known to engage in strong aggressive interactions, especially when competing for nest sites, and some degree of spatial segregation may result from this (Mikkola 1983). However, this situation is opposite to the barred owl invasion in the United States because the smaller tawny owl is expanding into the range of the larger Ural owl. The Great Grey Owl (*S. nebulosa*) is more distinct in range and habitat than the former two *Strix*, is more nomadic in following microtine cycles, less sedentary in winter, takes smaller prey, hunts somewhat more diurnally, and occupies larger breeding territories (ca. 650 ha). Predation by *S. nebulosa* on *S. uralensis* and by *S. uralensis* on *S. aluco* is known, but is apparently infrequent (Mikkola 1983).

In Asia, *Strix ocellata* and *S. selaputo* are similar in size (M/F approximate weights 690/870 g), and have abutting, allopatric ranges in India and Burma-Malaysia, respectively. Their combined range is shared with the larger *S. leptogrammica* (M/F weight 845/1055 g). Their size difference (a factor of 1.22) is much less than in most coexisting owls, but the species with overlapping geographic ranges are segregated largely by habitat, with the latter in dense tropical forest and the former two in more open, lightly-wooded country and plantations (König et al. 1999).

In South America several groups of *Strix/Ciccaba* species coexist. For example, in southeast Brazil and northeast Argentina, three *Strix/Ciccaba* species (*C. virgata*, *S. hylophila*, and *C. huhula*) occur sympatrically in lowland, humid forest, but their ecologies are not well known (del Hoyo et al. 1999). *C. virgata* (M/F weights 222/278 g) is the smallest, but the other two are similar in size (*S. hylophila* M/F weights 302/395 g; *C. huhula*, 329/411 g). In northwest South America and throughout Central America, *C. virgata* and *C. nigrolineata* are frequently sympatric in lowland rainforests (see above). No interactions between them nor differences in

habitat use have been recorded, but the two species have distinct diets (del Hoyo et al. 1999). *C. nigrolineata* is a bat-eating specialist, and *C. virgata* eats mostly small rodents (Ibañez et al. 1992; Gerhardt et al. 1994). Their difference in weight (by a factor of 1.78) presumably relates to hunting mode and diet differences, and clearly denotes a degree of ecological segregation sufficient for their coexistence. *C. virgata* extends north into Mexico, and from Nicaragua to Chiapas overlaps in range with *S. fulvescens*, which is much larger (by a factor of 2.29; M/F weights 506/640 g). A third *Strix* species, the barred owl is allopatric with *S. fulvescens*, a taxon with which it was previously considered conspecific.

In North America *Strix nebulosa* partially overlaps in range with more southerly and smaller species *S. varia* and *S. occidentalis* in a way similar to its overlap in northwestern Eurasia with *S. uralensis* and *S. aluco*. Interestingly, the size differences between the three North American *Strix* species parallel those of the European species: mean masses, north to south in western North America, are *nebulosa-varia-occidentalis* (974-717-621 g). Thus, the trio is closer interspecifically in mean mass than is the European trio (1080-785-475 g), since *S. aluco* is much smaller (475 g) than *S. occidentalis caurina* (610 g) and *S. nebulosa* is a little larger in Europe than North America. Unlike northwestern Europe, there was until recently (see below) relatively little sympatry in the North American *Strix*, with *S. nebulosa* occupying a geographic range north of and almost completely allopatric to *S. varia*, and only marginally sympatric with *S. occidentalis* in the Cascade Range and Sierra Nevada. Note that the size difference between *S. nebulosa* and *S. occidentalis* is large (factor of 1.6); but beyond this, *S. nebulosa* occupies the high-elevation, more open, subalpine woodland and meadow regions of the western mountains, whereas *S. occidentalis* occurs at lower elevations and in more contiguous and dense forest and woodland (Winter 1986; Johnsgard 2002). *S. nebulosa* is much closer in size to *S. varia* (factor of 1.36), but because both *S. varia* and *S. occidentalis* are species of forest and woodland in lowlands and foothills, there appears to be little in the way of

potential interaction between either of these two species and *S. nebulosa*.

While the recent invasion of the barred owl into the range of the northern spotted owl is our chief interest here, the two species are sympatric in south central Mexico and, presumably, have been sympatric there for a long time. *S. v. sartorii* and *S. o. lucida* are reported to occupy similar conifer and mixed woodlands, humid to semi-arid pine-oak and pine-fir, at similar elevations (1500–2500 m), although spotted owls may range lower (to 1200 m; Enríquez-Rocha et al. 1993; Howell and Webb 1995). However, we could find no published ecological studies of the barred owl subspecies in Mexico. *S. o. lucida* is the smallest of the three spotted owl subspecies. There is a trend for decreasing mass among the subspecies (Gutiérrez et al. 1995) north to south, which appears to continue within subspecies (M/F weights for *S. o. lucida* are 509/569 g for birds in Arizona, USA and New Mexico, USA; specimen records from the Museum of Vertebrate Zoology [Berkeley] show the masses of five male and four female *S. o. lucida* from Chihuahua, Mexico as 483 g ± 31.0 SD and 518 g ± 30.3 SD, respectively). Thus, birds at the southern end of the range of *S. o. lucida*, where it contacts *S. varia*, may be even smaller. On the other hand, *S. v. sartorii* is apparently the largest of the barred owl subspecies, with relatively larger bill and feet. No mass data on this subspecies have been published, but lineal measurements reported by Ridgeway (1914) suggest that *S. v. sartorii* may be around 1.39 times larger in mass than typical *S. v. varia*. If this estimate proves correct, coexisting *S. v. sartorii* at M/F weights of 878/1113 g (again, these masses are estimates from regression analysis based on Ridgeway's [1914] linear measurements) and *S. o. lucida* at M/F weights of 509/569 g, would differ in mass by a factor of almost two, which may facilitate coexistence of these two southern races (see also Gutiérrez et al. 2004). This contrasts with the much more similar masses of *S. v. varia* and *S. o. caurina* in the Pacific Northwest, where *S. v. varia* is the smallest barred owl subspecies and *S. o. caurina* is the largest spotted owl subspecies. The result of our regression estimate is opposite to predictions based on biogeographic rule (i.e., animals decrease in size from north to south), but

they are the best we have at this time because there are very few museum specimens of these owls from Mexico. In the Pacific Northwest, the two differ in mass by a factor of about 1.8, which may be too small a difference to permit coexistence by dint of size and size-related ecology alone. In this area it might be expected that range differentiation would result from the evolution of habitat use differences (i.e., forest type or elevation), as is the case in similarly-sized sympatric *Strix* elsewhere. Thus, from our assessment of world-wide patterns of coexistence of owls, theory predicts that strong competition should occur between barred owls and northern spotted owls in their new area of sympatry, and that their stable coexistence seems unlikely.

Empirical evidence

Breeding biology

Barred owls have a larger range of clutch sizes than northern spotted owls (1–5 vs. 1–3; Gutiérrez et al. 1995; Mazur and James 2000). However, it is not clear that they produce more young on average than spotted owls (i.e., are more productive than spotted owls in the Pacific Northwest). For example, in a study with a limited sample size in Washington, productivity (number of young per successful nest) of barred owls ranged from 1.85 ($n = 6$) to 2.29 ($n = 7$; Hamer 1988). Several pairs in Hamer's (1988) 3-year study produced young every year while others did not produce any young. However, these birds did produce more young than a sympatric group of spotted owls. Estimates of barred owl productivity taken from the literature ranged from 1 to 2.4 young per successful nest (Mazur and James 2000), whereas mean estimates of productivity for spotted owls ranged from 1.5 to 2.1 young per successful nest (Forsman et al. 1984). However, reproductive output (number of young fledged per pair) would be a more meaningful comparison of reproductive performance between the two species; such data is lacking for the barred owl but not for the spotted owl (Anthony et al. 2006). Barred owl reproductive activity appears to be quite variable

from year to year, which is similar to spotted owls (Mazur and James 2000).

Home range and habitat use

Barred owls have smaller home ranges than spotted owls in Washington (321–644 ha for breeding and annual ranges; Hamer 1988). In the Washington Cascades, spotted owl home ranges east of Mt. Baker were 3.5–7.4 times larger than barred owl home ranges (Hamer et al. 1989). Spotted owls in Washington also have the largest home ranges among northern spotted owl populations (range = 2060–4020 ha, $n = 23$ pairs and 11 individuals; Gutiérrez et al. 1995). There are no estimates of barred owl home range size in Oregon and California, but spotted owl home ranges vary from 520 to 2590 ha ($n = 42$ pairs and 19 individuals) in Oregon and from 370 to 1030 ha ($n = 2$ pairs and 48 individuals) in California (Gutiérrez et al. 1995). Given the home range of the two species when in sympatry, the differences suggest that the barred owl either has superior ability to exploit more resources in a small area within the same habitat or to access additional resources that are unavailable to the spotted owl.

Although ecological studies of barred owls in the Pacific Northwest, USA are limited (Mazur and James 2000), initial reports suggested that barred owls were more strongly associated with younger forest types than were spotted owls (e.g., Hamer 1988; Iverson 1993). However, subsequent reports have shown that barred owls used a variety of habitats, including mature or old-growth forests that were typically occupied by spotted owls (Dunbar et al. 1991; Dark et al. 1998; Herter and Hicks 2000; Pearson and Livezey 2003; Kelly et al. 2003). Moreover, the two species use the same types of nests (Forsman et al. 1984; Hamer 1988; Devereux and Mosher 1984; Postupalsky et al. 1997).

Barred owls may initially colonize riparian areas (i.e., moister habitats), but once they are established they will move into relatively less mesic sites (Gutiérrez et al. 2004). However, “drier” sites on the Olympic Peninsula and Washington Cascades where this expansion of habitat use has been reported are more mesic than drier habitats that are occupied by spotted

owls in other areas (e.g., Klamath Province of Oregon and California). So it is unclear if the expansion of barred owls into inland areas of the Klamath Province will be impeded by the dry conditions of interior forests and woodlands or if they will ultimately expand to all habitats occupied by spotted owls. Because of this potential and because barred owls are known to use almost the entire range of habitats typical of spotted owls, some degree of competition between the species seems inevitable because they have large diet overlap (see below). However, coexistence may be possible if northern spotted owls occupy habitat outside of the preferred habitat of barred owls. Nevertheless, we currently do not know if habitat segregation will occur between these species such that coexistence in some areas will be possible.

Food use and foraging

Northern spotted owls are food specialists, preying almost exclusively on medium-sized small mammals, particularly northern flying squirrels (*Glaucomys sabrinus*), dusky-footed woodrats (*Neotoma fuscipes*) and bushy-tailed woodrats (*N. cinerea*) (Gutiérrez et al. 1995). The dominance of these three prey species can vary by area, and spotted owls may eat other small mammals in some regions (Gutiérrez et al. 1995; Forsman et al. 2004). In contrast, barred owls are food generalists throughout their range (Korschgen and Stuart 1972; Smith et al. 1983; Marks et al. 1984; Devereux and Mosher 1984; Cook 1992; Dodd and Griffey 1997). Where spotted owls and barred owls are sympatric, there is considerable diet overlap in the number of species taken (76%; Hamer et al. 2001). However, barred owls eat many species associated with riparian and other moist habitats such as fish and frogs and tend to take more diurnal prey than spotted owls, whereas spotted owls take more arboreal and semi-arboreal prey (Hamer et al. 2001). These observations suggest that barred owls have similar prey selection but greater breadth of foraging strategies than spotted owls. In addition, barred owls took a much lower proportion of the four primary prey species taken by spotted owls in Hamer et al. (2001;

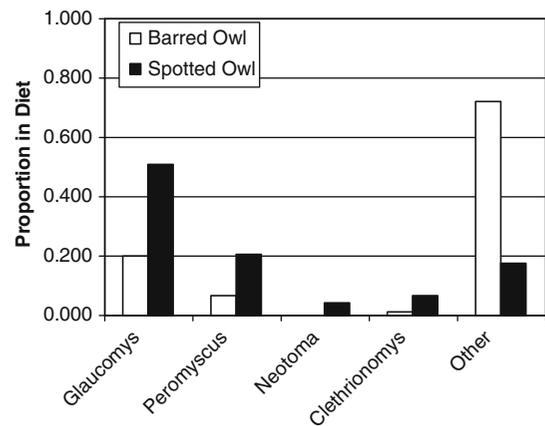


Fig. 2 Relative frequency of top 4 prey (and all other prey summarized as “other”) taken by spotted owls in the diet of sympatric barred and spotted owls in the state of Washington, USA (data taken from Hamer et al. 2001)

Fig. 2). This suggests that barred owls may only be opportunistically taking spotted owl prey and not necessarily selecting for the same prey species as spotted owls.

The consequences of similar diets and broader foraging areas and methods by barred owls are that barred owls may sufficiently reduce the density of spotted owl prey (small mammals) such that the smaller owl cannot find sufficient food for maintenance and reproduction. This scenario is plausible given that spotted owls apparently can depress flying squirrel abundance (Carey et al. 1992), and spotted owl reproduction is influenced by prey abundance (Rosenberg et al. 2003). Hence, indirect competition through resource depletion of shared prey may be a factor in determining whether the two owl species can coexist.

Interference competition and aggressive interactions

There is anecdotal evidence that barred owls behave aggressively toward spotted owls including agitated vocal responses to spotted owl calls, physical attacks on spotted owls and predation, whereas reciprocal agonistic behavior seems to occur less often (Leskiw and Gutiérrez 1998; review in Gutiérrez et al. 2004). This has

led to the hypothesis that barred owls are behaviorally dominant to spotted owls, which predicts that spotted owls would tend to be less vocal in the presence of barred owls (Hamer 1988; Kelly et al. 2003). Limited experimental evidence tends to support this hypothesis (Crozier et al. *in review*). If such behavior patterns are typical of the species' interactions, it could lead to interference competition in terms of social behavior, nest site selection, habitat selection and territory occupancy. However, another prediction following from the behavioral suppression hypothesis is that recapture rates of spotted owls on long-term demographic studies should decline as barred owls increase on these study areas, which has not occurred (Anthony et al. 2006).

Northern spotted owls have been declining in several areas of their range over the past two decades (Anthony et al. 2006). In some areas such as the Olympic Peninsula, this decline has been dramatic. At the northern edge of the northern spotted owl's range, there were four times more barred owl sites than northern spotted owl sites in British Columbia during the late 1980s (Dunbar et al. 1991). However, there has also been considerable loss of spotted owl habitat through intensive timber harvesting in British Columbia, which confounds the problem (Dunbar et al. 1991). Both field studies (Pearson and Livezey 2003; Kelly et al. 2003) and unpublished observations (summarized in Gutiérrez et al. 2004) have suggested that barred owls have been actively displacing spotted owls from their territories. In all areas showing spotted owl decline there has been a concomitant increase in barred owls. However, there have been a few cases where presumed displacement of spotted owls has occurred, but where spotted owls recolonized the sites. Unfortunately, rates of recolonization cannot be easily calculated because once a spotted owl disappears from a site, the site is often excluded from future monitoring (see Gutiérrez et al. 2004). In addition, many vacant spotted owl sites have not been recolonized by either species (Herter and Hicks 2000; Wiedemeier and Horton 2000). Large numbers of vacant sites would not be expected if the main cause of spotted owl decline is barred owl

invasion and preemption of suitable sites. Vacant territories suggest alternative explanations for the spotted owl decline such as habitat loss (USDI 1990), but habitat is still present in some areas where declines have been severe (e.g., Olympic National Park contains primarily pristine forest). Yet, despite the presence of habitat, neither the quality of such habitat nor the influence of potential lag effects due to past habitat loss are known. Further, these results are consistent with other factors that are known to negatively affect spotted owls. For example, Franklin et al. (2000) predicted, based on past weather data, that there could be long periods of decline in a spotted owl population due solely to weather effects. All of these observations are correlative and do not prove causality. Moreover, declines of spotted owls are confounded by many potential causes. Thus, it seems that a critical experiment is needed to determine whether or not the increase of barred owls is causing the decline in spotted owls (see below).

Hybridization

Hybridization between barred and spotted owls is relatively uncommon although more than 50 cases of interspecific hybridization have been documented from 1974–1999 (Hamer et al. 1994; Gutiérrez et al. 1995; Dark et al. 1998; Kelly 2001). Some of these cases were backcrosses (Hamer et al. 1994; Gutiérrez et al. 1995; Kelly and Forsman 2004) suggesting potential for genetic introgression. Thus, the extent of introgression is likely to be higher than the level indicated by the >50 documented cases, unless later generation backcrosses are less viable.

Even though these two species are differentiated genetically, morphologically (both in plumage characteristics and in body size) and, to some extent, behaviorally and ecologically (Gutiérrez et al. 1995; Barrowclough et al. 1999; Mazur and James 2000), there appears to be few strong isolating mechanisms. Hybridization is often more prevalent when one species is rare or limiting (Randler 2002) or when one species is a recent invader of new habitat (Randler 2002; Riley et al. 2003). Thus, as spotted owls become rarer, they

are probably more likely to mate with barred owls, especially if barred owls are more common. This may already be an important threat in areas such as southern British Columbia where spotted owls are already rare and barred owls are abundant. Gee (2003) also suggests that in some hybrid zones the two species may mix randomly. Thus, hybridization with barred owls, although it may not be common now, may be an increasing threat to spotted owls as the latter becomes rarer and the former more common in both absolute and relative terms. However, the rate of hybridization may be partially related to the sex ratio of owls in a population because of reversed sexual dimorphism and the fact that male barred owls are close to the size of female spotted owls (Kelly and Forsman 2004).

Discussion

Prognoses for the future

Barred owls have rapidly colonized essentially the entire range of the northern spotted owl. Based on our assessment of ecological segregation among owls, we predict that the barred owl will have negative impacts on the threatened spotted owl through competitive exclusion. This prediction is also supported by anecdotal evidence of aggressive heterospecific interactions (review in Gutiérrez et al. 2004), ecological observations of relative habitat (references cited above), and experimental evidence of possible behavior dominance (Crozier et al. in review). Dietary relationships (Fig. 2) suggest that interference competition would more likely be the mode of this relationship rather than contest competition. This contention is supported by modeling of empirical data, which has shown that there is a negative correlation between barred owl presence and spotted owl fecundity (Olson et al. 2004) and site occupancy (Olson et al. 2005). On the other hand, we do not know in detail, or with any degree of precision, the rate of barred owl range expansion, the magnitude of the increase of population density, the rate of colonization of different forest types

or the nature of interspecific interactions. More importantly, we do not know if declines in spotted owl populations are being caused or simply exacerbated by barred owls (Anthony et al. 2006).

Despite the unambiguous warnings and suggestions for evaluating the impact of barred owls on spotted owls presented in the listing decision for the spotted owl (Anderson et al. 1990) and in the draft spotted owl recovery plan (USDI 1992), there have been very few studies specifically designed to evaluate the interspecific interactions between these two species. Most information on these interactions and on barred owl population increase has been collected incidental to spotted owl research (Gutiérrez et al. 2004). Despite the paucity of information, many biologists now feel that the barred owl is the most serious current threat to the spotted owl. Yet, because of the substantial uncertainty, it is impossible to predict with a high level of accuracy or confidence the ultimate impact of the barred owl on the spotted owl in the Pacific Northwest. However, it is apparent that the barred owl appears to be having negative impacts on the spotted owl (Gutiérrez et al. 2004; Anthony et al. 2006; Olson et al. 2004, 2005). It is also clear from our examination of patterns among coexisting owl species that these two species will be strong competitors, with the larger barred owl likely being competitively superior to the smaller spotted owl because they do not segregate strongly by habitat. Because of these observed or predicted relationships between species, Gutiérrez et al. (2004) developed a series of hypotheses about the direction and magnitude of the barred owl's effect on the spotted owl. These hypotheses express a continuum of outcomes, ranging from extinction of the northern spotted owl to its persistence only in specific areas where they are maintained through management intervention (e.g., removal of barred owls).

Barred owls occupy many habitat types, including old growth forests (Gutiérrez et al. 2004). By contrast, spotted owls appear to be more closely associated with either old growth forest or forests that are structurally complex (Gutiérrez et al. 1995). Timber harvest may have increased interpolation and contact of the

two species' preferred and potential habitats, which may lead to increased potential for competition between the species. However, some forest heterogeneity has been associated with site occupancy, higher survival and higher reproduction in portions of the spotted owl range that have naturally dynamic disturbance regimes (Franklin et al. 2000; Franklin and Gutiérrez 2002; Olsen et al. 2004). Thus, it is unclear what role anthropogenic habitat alteration has played in promoting contact between the two species.

It is unknown whether the barred owl invasion has reached its peak over most of the northern or California spotted owl's ranges, and thus, it is unknown whether the effects of barred owls on spotted owls have been fully realized. However, there is also no evidence that the barred owl's increase will be followed by a collapse (Simberloff and Gibbons 2004). In areas where barred owls are low in number, it is possible that they are simply in the colonization phase of invasion, from which they will rapidly expand when they reach a critical threshold density. Alternatively, there is a continuum from mesic to xeric forest types within the spotted owl range which may prevent barred owls attaining high densities in the drier forests occupied by spotted owls (Gutiérrez et al. 2004). For example, Peterson and Robins (2003) developed a predictive model on the geographic spread of barred owls based purely on habitat characteristics, which predicted that barred owls will colonize the range of the northern spotted owl, but will not invade very far south into the range of the California spotted owl. We now know that the barred owl has spread not only throughout the northern spotted owl range but also throughout most of the Sierra Nevada range of the California spotted owl, although they currently are at very low densities (Seamans et al. 2004). While it is important to assess the barred owl population trends in the invasion area of western North America, we believe the only unambiguous and expedient way to link the barred owl increase with the spotted owl decrease is to conduct experiments which involve removal of barred owls. Such experiments have a long-standing history in endangered species management (Ortega et al. 2005).

Options for conservation: the conundrum

The widespread presumption that the barred owl is replacing the spotted owl on a large scale is confounded by potential effects of habitat change (such as cumulative or lag effects associated with historic changes or reduction in habitat quality), year-to-year weather effects on spotted owl population trends via reduced reproduction and decreased adult or juvenile survival. Evidence suggests that the barred owl is having a negative effect on the northern spotted owl in some areas, but in other areas the barred owl has not yet had an effect because either the conditions are not entirely suitable for its occupation or it has not yet reached a critical density when impacts to spotted owls would occur. Although it will be important to monitor changes in barred owl numbers, particularly where they are in low density, it will only provide additional correlative information on spotted owl declines. Therefore, we cannot be certain of the ultimate outcome of the interspecific interactions between the two species without critical experiments.

Despite the many uncertainties about their interspecific interactions, we believe that observational studies designed to evaluate these interactions will not provide unambiguous answers to the critical question of whether or not barred owls are causing current declines in spotted owl numbers. Such interaction studies could provide some useful information for managers once it has been demonstrated experimentally that barred owls are causing spotted owl declines (Simberloff 2003). Observational or correlative studies designed to evaluate interactions between these species have limited inferential capability because they are confounded with other factors known to influence spotted owl population dynamics such as habitat and weather (Franklin et al. 2000; Gutiérrez et al. 2004). In addition, there could be possible changes in detectability of spotted owls over time when barred owls are present (Anthony et al. 2006; Crozier et al. in review). Hence, it is critical to take an experimental approach, rather than an observational one. We also have a unique opportunity—never in the history of conservation has a threatened species had the information base from which to launch such a critical experiment.

There are many very large spotted owl population studies, which are replicated in space. Some of these study populations are exhibiting steep declines documented by 20+ years of mark-recapture data, and would provide the ideal context for critical removal experiments (see below, Anthony et al. in press). It is such critical experiments that are lacking in wildlife management and conservation (Romesburg 1981).

In the case of invading barred owls, one critical experiment would be the removal of barred owls from areas where long-term spotted owl demographic studies exist, and where major spotted owl declines are occurring simultaneously with rapid increases in barred owls (Anthony et al. 2006). The long-term demographic studies on spotted owls provide estimates of survival, reproduction, recruitment, and rates of population change during the barred owl invasion and, therefore, have the necessary pre-treatment component for a removal study. Clearly, lethal control is not only the most cost-effective way to remove barred owls but currently it is probably the only practical method. Correctly executed removal experiments should provide an unambiguous result regarding the effect of barred owls on spotted owl population declines. There are many other studies and management options that could be implemented, but no observational studies have the potential to ascertain cause and effect relationships like a removal experiment. We feel the timing for such a removal experiment is critical for the survival of the spotted owl.

It is considered routine to control invasive species, particularly plants and pests. Vertebrates also are frequently the object of control efforts when they are invasive (Ortega et al. 2005). Herein lies the conundrum in the case of the barred owl—it is a native species which is expanding its range, and in that process may negatively impact an endangered species. Regardless of whether it is a natural expansion or one facilitated by humans, the barred owl is a species of owl native to North America. Such a dilemma is not without precedent in endangered species conservation, but the complexity and scale

appears to be (Courchamp et al. 2003). An unresolved barred owl/spotted owl issue provides an opportunity either for inaction by regulatory agencies or for advocacy to mislead the public (e.g., Peterson 2006). Owls, in addition to holding special places in human mythology (Marcot and Johnson 2003), are predators, thus raising their status in terms of human perceptions. These facts suggest that opposition is likely to emerge against either removal experiments or control efforts (if control should be recommended following the results of removal experiments). Such resistance could involve legal action, withholding research funds, or focusing efforts and funds on studies of the interactions between the species. While it is appropriate to scrutinize every control effort of an invasive species whether native or alien, it seems evident to us that carefully designed removal experiments are our best hope for rapidly determining whether declines in some spotted owl populations are being caused by barred owls. Many native species are controlled in the United States to benefit endangered species or species of interest to humans. Even among biologists working with spotted owls there is trepidation or resistance about the prospect of either engaging in removal experiments or, ultimately, control efforts. Although we feel these reactions are emotionally understandable, we think they are misplaced, and do not serve a scientific leadership function for the public. As scientists concerned with endangered species or invasive species, we feel that the only way to inform the public of their full range of options is to understand the effect of barred owls on spotted owls by experimentally removing barred owls from areas where spotted owls are declining to determine whether they are the root cause of the declines.

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Appendix

Appendix 1 Examples of coexisting owl species, over a range of habitats and geographical regions. Codes A–U are used in Figure 1

Code	Region	Habitat	Species	Reference
A	Missouri, USA	Hardwood forest	<i>Bubo virginianus virginianus</i> <i>Megascops asio</i> <i>Strix varia varia</i>	Korschgen LJ and Stuart HB 1972.
B	California, USA	Oak woodland	<i>Tyto alba</i> <i>Bubo virginianus pacificus</i> <i>Glaucidium californicum</i> <i>Megascops kennicottii</i>	Root 1969
C	California, USA	Oak woodland	<i>Tyto alba</i> <i>Bubo virginianus pacificus</i> <i>Megascops kennicottii</i>	Cody (Pers. Obs.)
D	California, USA	Foothill oak-pine	<i>Bubo virginianus pacificus</i> <i>Megascops kennicottii</i>	Cody (Pers. Obs.)
E	Wyoming, USA	Lodgepole pine forest	<i>Strix occidentalis occidentalis</i> <i>Aegolius acadicus</i> <i>Asio otus</i> <i>Strix nebulosa</i>	Cody (Pers. Obs.)
F	Arizona, USA, Mexico	Sonoran Desert	<i>Asio otus</i> <i>Bubo virginianus pallescens</i> <i>Micrathene whitneyi</i> <i>Megascops kennicottii aikeni</i>	Cody and Velarde 2002
G	Colima, Mexico	Montane pine-oak woodland	<i>Asio stygius</i> <i>Glaucidium gnoma</i> <i>Megascops trichopsis</i> <i>Strix occidentalis lucida</i> <i>Ciccaba virgata</i>	Schaldach 1963
H	Veracruz, Mexico	Montane mixed oak woodland	<i>Glaucidium brasilianum</i> <i>Pulsatrix perspicillata</i> <i>Ciccaba virgata</i>	Howell 1999
I	Chiapas, Mexico, CR	Lowland rainforest	<i>Glaucidium griseiceps</i> <i>Megascops guatemalae</i> <i>Ciccaba nigrolineata</i> <i>Ciccaba virgata</i>	Howell 1999
J	Guatemala	Lowland rainforest	<i>Glaucidium brasilianum</i> <i>Megascops guatemalae</i> <i>Ciccaba nigrolineata</i> <i>Ciccaba virgata</i>	Land 1963
K	Costa Rica	Lowland rainforest	<i>Glaucidium griseiceps</i> <i>Lophostrix cristatus</i> <i>Megascops guatemalae</i> <i>Pulsatrix perspicillata</i> <i>Ciccaba nigrolineata</i> <i>Ciccaba virgata</i>	Enriquez Rocha and Rangel-Salazar 2001
L	Andes, Peru	Montane woodland 2500m elev.	<i>Glaucidium jardinii</i> <i>Megascops albogularis</i> <i>Ciccaba albitarsis</i>	Graves 1985
M	Andes, Peru	Premontane woodland, 2000m	<i>Megascops ingens</i> <i>Megascops marshalli</i> <i>Ciccaba albitarsis</i>	Graves 1985
N	Peru	Lowland rainforest	<i>Xenoglaux loweryi</i> <i>Glaucidium hardyi</i>	Terborgh et al. 1990

Appendix 1 continued

Code	Region	Habitat	Species	Reference
			<i>Lophotrix cristatus</i>	Lloyd 2003
			<i>Megascops watsoni</i>	
			<i>Pulsatrix perspicillata</i>	
			<i>Ciccaba huhula</i>	
			<i>Ciccaba virgata</i>	
O	Cuba	Forest	<i>Asio stygius</i>	Garrido and Kirkconnell 2000
			<i>Glaucidium siju</i>	
			<i>Gymnoglaux lawrencei</i>	
P	SE Europe	Oak woodland	<i>Asio otus</i>	Cody, Pers. Obs.
			<i>Bubo bubo</i>	
			<i>Otus scops</i>	
			<i>Strix aluco</i>	
Q	Africa	Dry woodland	<i>Bubo africanus</i>	Voous 1966
			<i>Bubo lacteus</i>	
			<i>Glaucidium perlatum</i>	
			<i>Otus leucotis</i>	
			<i>Otus senegalensis</i>	
R	West Africa, Cameroon	Rainforest	<i>Tyto alba</i>	Languy and Motombe 2003
			<i>Glaucidium tephronotum</i>	
			<i>Otus senegalensis</i>	
			<i>Strix woodfordi</i>	
S	Madagascar	Forest	<i>Tyto soumagnei</i>	Langrand 1990
			<i>Asio madagascariensis</i>	
			<i>Otus rutilus</i>	
T	Pakistan	Indus forest	<i>Bubo bubo</i>	Roberts 1991
			<i>Glaucidium cuculoides</i>	
			<i>Otus spilocephalus</i>	
			<i>Strix aluco</i>	
U	SE Australia	Forest	<i>Tyto novaehollandiae</i>	Loyn et al. 2001
			<i>Tyto tenebricosa</i>	
			<i>Ninox connivens</i>	
			<i>Ninox strenua</i>	

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