

Distributional Dynamics of Invasion and Hybridization by *Strix* Spp. in Western North America

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CHAPTER 5

DISTRIBUTIONAL DYNAMICS OF INVASION AND HYBRIDIZATION BY *STRIX* SPP. IN WESTERN NORTH AMERICA

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ABSTRACT.—Understanding how hybridization may affect extant and emerging taxa requires knowledge of the origins, viability, and breeding tendencies of hybrid individuals. We examined the geographic and environmental underpinnings of invasion and hybridization among native North American members of the genus *Strix*. In the early 20th century, the Barred Owl (*S. varia*) started expanding westward through southern Canada. Since 1973, the species has been invading habitats of the Spotted Owl (*S. occidentalis*), usually displacing but occasionally hybridizing with two Spotted Owl subspecies (*S. o. occidentalis* and *S. o. caurina*) to yield viable offspring that often disperse long distances before breeding. Given the high dispersal capabilities of the hybrids, questions remain as to whether hybrid offspring are preferentially colonizing environments that are characteristically different from their natal territories. Further questions surround the proximate origins of the Barred Owl range expansion. We show that the westward range expansion of the Barred Owl was spatiotemporally concomitant with historical increases in summer temperature and that the expansion corridor was positioned at relatively high latitudes because of habitat restrictions. These results provide quantitative support to previous claims that the Barred Owl range expansion was largely shaped by natural processes. We also show that first filial Barred × Spotted hybrid owls occupy similar environments before and after postnatal dispersal and are randomly distributed both geographically and climatically with respect to parentals. We discuss the climatic mechanisms that may be influencing these dynamics, and conclude with implications for conservation of *Strix* spp. Received 5 July 2006, accepted 5 February 2007.

RESUMEN.—Para entender cómo la hibridación puede afectar a taxones existentes y emergentes, se necesita conocer los orígenes, la viabilidad y las tendencias de apareamiento de los individuos híbridos. En este trabajo, examinamos las bases geográficas y ambientales de la invasión e hibridación entre miembros del género *Strix*, nativos de Norte América. A principios del siglo 20, *S. varia* comenzó a expandirse desde el oeste hacia el sur de Canadá. Desde 1973, la especie ha invadido habitats de *S. occidentalis*, generalmente desplazándolo, aunque ocasionalmente hibridando con dos de sus subespecies (*S. o. occidentalis* y *S. o. caurina*) y produciendo una progenie viable que normalmente se dispersa a grandes distancias antes de reproducirse. Dada la gran capacidad de dispersión de los híbridos, nos preguntamos si su descendencia coloniza preferentemente ambientes distintos de sus territorios de origen. Cabe también preguntarse por el origen de la expansión del rango de *S. varia*. Nuestros resultados muestran que la expansión de su rango hacia el oeste está relacionada históricamente con un aumento de las temperaturas estivales; además, el corredor de la expansión se localizó a latitudes altas, esto debido a restricciones en el hábitat. Estos resultados apoyan cuantitativamente las hipótesis de que la expansión del rango de distribución de *S. varia* estuvo determinada por procesos naturales. Además, mostramos que los híbridos descendientes del cruce *S. varia* × *S. occidentalis* ocupan ambientes similares, tanto climática como geográficamente, al de los parentales, presentando, además, una distribución aleatoria. Discutimos los mecanismos climáticos que podrían estar influenciando estas dinámicas y concluimos con implicaciones para la conservación de *Strix*.

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INVADING SPECIES CAN exert evolutionary influences on resident species through a variety of processes, including physical or niche displacement, demographic breakdown, and hybridization (Mooney and Cleland 2001). Most controversial is the role of hybridization (O'Brien and Mayr 1991, Allendorf et al. 2001). On one hand, hybridization has been associated with many plant and animal extinctions (Rhymer and Simberloff 1996); on the other, it has generated new species (V. Grant 1966, Arnold 1992, Bullini 1994, Rieseberg 1997, Seehausen 2004). Some studies have suggested that hybridization is rare (Dowling and Secor 1997), whereas others have concluded that it is common (Grant and Grant 1992).

Hybridization can act to influence evolutionary trajectories in six major ways, broadly related to whether the causal mechanism is natural or anthropogenic, whether hybrids are fit and fertile, and, if they are fertile, whether they breed with other hybrids or parentals (Arnold and Hodges 1995, Allendorf et al. 2001). Anthropogenically mediated hybridization can result directly from species introductions (e.g., Rhymer et al. 1994) or indirectly via environmental perturbations (e.g., Simons et al. 2001). Unfortunately, it is often difficult in practice to clearly distinguish natural origins from indirect human influences, as is evident with the red wolf (*Canis rufus*; Wayne and Jenks 1991, Wilson et al. 2000). However, such distinctions may be critical, because misclassifications can lead to the failure to protect "natural" biodiversity (Allendorf et al. 2001).

We investigated the geographic and environmental characteristics of invasion and hybridization by *Strix* spp. in western North America. Native to eastern North America, the Barred Owl (*S. varia*) started expanding west from the midwestern United States through southern Canada in the early 1900s (Houston and McGowan 1999). The species first contacted the northern range limit of the Spotted Owl (*S. occidentalis*) in southwestern Canada around 1973 (Taylor and Forsman 1976) and now occurs in western North America from British Columbia south to northern California, largely overlapping the range of the Northern Spotted Owl (*S. o. caurina*) and partially overlapping the range of the California Spotted Owl (*S. o. occidentalis*) (Haig et al. 2004a, Barrowclough et al. 2005). A third well-supported subspecies (Barrowclough

and Gutiérrez 1990; Barrowclough et al. 1999; Haig et al. 2001, 2004a), the Mexican Spotted Owl (*S. o. lucida*), remains allopatric with the congeners (Fig. 1). Both *S. o. caurina* and *S. o. lucida* are formally listed as threatened under the U.S. Endangered Species Act (U.S. Fish and Wildlife Service 1990, 1993). Hence, the expansion of the Barred Owl in western North America has important implications for Spotted Owl conservation.

Field observations suggest that Barred Owls, generally the larger and more aggressive of the two species, are in most instances displacing or killing Spotted Owls (Leskiw and Gutiérrez 1998, Kelly et al. 2003, Olson et al. 2005). However, occasionally the species hybridize (Hamer et al. 1994), with almost all pairings involving male Spotted Owls mated to female Barred Owls (Haig et al. 2004b), as predicted from patterns of reverse sexual size-dimorphism (females larger than males; Kelly and Forsman 2004). Apparently, current levels of hybridization are low enough that they do not seriously threaten the conservation status of either species (Haig et al. 2004b, Barrowclough et al. 2005), though hybrids are known to back-cross with parentals and questions remain about actual hybrid prevalence.

The origins of the Barred Owl's range expansion remain unknown. A distribution model using the environmental attributes of the species' eastern range accurately predicted the existence of suitable western habitats where the Barred Owl now occurs (Peterson and Robbins 2003). The model predicted extensive geographic overlap between *S. varia* and *S. o. caurina*, as well as partial geographic overlap with *S. o. occidentalis* and *S. o. lucida*. However, the model failed to delineate the Canadian expansion corridor, which suggests that the early phases of the Barred Owl movement were not simply the result of a demographic expansion through suitable habitats. Other studies have concluded that the range expansion was natural in origin but fueled by either adaptation to coniferous forests (Boxall and Stepney 1982) or historical climate change (Johnson 1994). However, the Barred Owl expansion may have been influenced by anthropogenic factors, including changes in forest management practices (Root and Weckstein 1994) or the establishment of wooded riparian areas in the Great Plains (Dark et al. 1998).

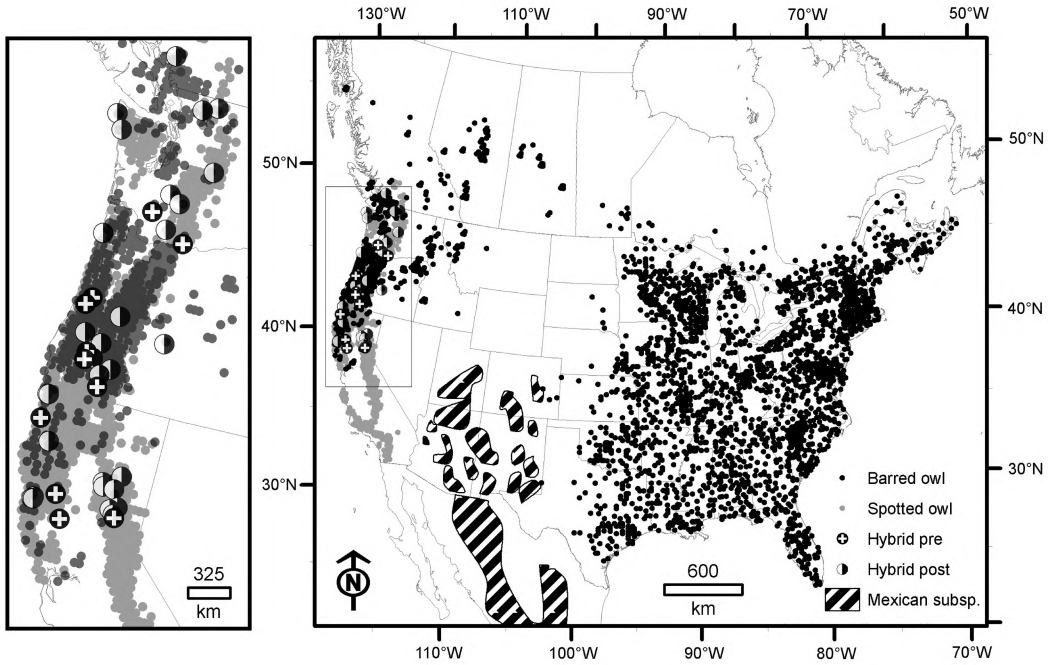


FIG. 1. Observations of Spotted, Barred, and hybrid owls (before and after postnatal dispersal) in North America. The Mexican Spotted Owl (*S. o. lucida*) was not included in the present study (range map obtained from NatureServe; map projection: Albers equal-area conic).

If hybridization in *Strix* represents a largely natural phenomenon tied to the ebb and flow of closely related species' distributions in space and time (Johnson 1994), conservation of these dynamics ultimately requires sound knowledge of the factors that determine where hybrids form, live, and breed. Recent empirical and theoretical work has shown that hybrids possessing extreme phenotypes that enable them to aggregate in physical and novel environmental spaces can become reproductively isolated from parentals and speciate over short evolutionary time-scales (McCarthy et al. 1995, Rieseberg 1997, Buerkle et al. 2000, Lexer et al. 2003, Rieseberg et al. 2003). New phenotypes sometimes appear only after several generations (Rieseberg and Ellstrand 1993). During that period, especially if hybrids remain locally codistributed with parentals, backcrossing can result in the differential shuffling of chromosomal regions between parental taxa (Rieseberg et al. 1995, 1996, 1999). When acted on by selection, such novel genetic variation has been shown to facilitate parental niche expansion (Choler et al. 2004).

Conversely, hybridization in *Strix* could negatively affect parental taxa. Simulations

have shown that extinction is a likely outcome of hybridization when reproductive barriers between parentals are weak and the native taxon is both rare and a poor competitor compared with the invader (Wolf et al. 2001). These three factors apply to *Strix* (Burnham et al. 1996, Kelly et al. 2003, Kelly and Forsman 2004, Olson et al. 2005). Extinction is also likely when parental and hybrid taxa occupy similar niches (Wolf et al. 2001). Although Barred and Spotted owls presently occupy similar habitats in western North America, high dispersal capabilities potentially enable the owl hybrids to colonize and breed in areas that are markedly different from their natal environments. Spotted Owls exhibit obligate natal dispersal (Gutiérrez et al. 1995), and we assume that hybrids are similar in this regard. Anecdotally, one hybrid banded as a juvenile was resighted as an adult 292 km away from its natal territory (Forsman et al. 2002). Locations of hybrids before and after postnatal dispersal may thus be distributed either randomly or nonrandomly in geographic or environmental space. Evidence of clustering of hybridization events would suggest an environmentally induced demographic basis

for parentals to meet and hybridize, whereas aggregation of adult hybrids would suggest that effective dispersal is nonrandom and capable of promoting ecological isolation. We examine these two possibilities and assess whether the Barred Owl's range expansion was spatiotemporally concomitant with early-20th-century climate change affecting areas with coniferous forests.

METHODS

Owl data.—Spotted, Barred, and first-filial-hybrid owl data were compiled from multiple sources, including state and federal (Sauer et al. 2003, Gustafson et al. 2004) wildlife agencies, natural-history museum collections (Burke Museum of Natural History, California Academy of Sciences, Los Angeles County Museum of Natural History, and Museum of Vertebrate Zoology, accessed through ORNIS; see Acknowledgments), and the literature (J. Grant 1966, Reichard 1974, Taylor and Forsman 1976, Boxall and Stepney 1982, Sharp 1989, Dunbar et al. 1991, Hamer et al. 1994, Dark et al. 1998, Kelly 1999, Kelly et al. 2003, Kelly and Forsman 2004). Second-generation hybrids were excluded from the analysis because of potential assignment errors (Haig et al. 2004b, Kelly and Forsman 2004). Non-georeferenced point-occurrence data with locality descriptions were georeferenced using the method described by Wieczorek et al. (2004). Additional localities were extracted from scanned and georeferenced original point-distribution maps (Kelly 1999, Kelly et al. 2003). Spatial uncertainty of georeferenced coordinates was small in relation to the spatial resolution of the analyses. Point data sets were generalized to a 10-minute spatial resolution to reduce the potential of sampling bias affecting our results. The final data set consisted of 959 Spotted Owl localities (672 *S. o. caurina*, 287 *S. o. occidentalis*; we did not consider *S. o. lucida* in the present analysis), 2,902 Barred Owl localities, and 41 hybrid localities, including 11 "juvenile" and 30 "adult" locations (Fig. 1). In all cases, hybrid age categories were determined unambiguously from the average age of owl natal dispersal (September of hatching year; Forsman et al. 2002).

Origins of the Barred Owl invasion.—Johnson (1994) hypothesized that the Barred Owl range expansion was facilitated by regional increases in mean summer temperature and precipitation. These changes are believed to have allowed the expansion "corridor" to become climatically more similar to the putative "source" areas. We used mean monthly temperature and precipitation data from June, July, and August (Mitchell and Jones 2005) to estimate changes in summer temperature and precipitation during the period (1901–1970) when the Barred Owl was expanding

through southern Canada. To estimate changes in these climate variables, we used means of two 10-year time blocks: 1901–1910 (i.e., "historical," at the beginning of the westward expansion) and 1961–1970 ("modern," when the species reached the Pacific Coast). These periods were long enough to smooth over interannual variation in temperature and precipitation. Barred Owl observations from the expansion corridor (Manitoba, Saskatchewan, Alberta, and British Columbia; $n = 133$) and from putative source populations (95–85°W and 45–50°N, which included southwestern portions of Ontario and northern portions of Minnesota, Wisconsin, and Michigan; $n = 129$), were used to assess whether regional patterns of summer warming and increased precipitation caused corridor and source locations to become climatically more similar. We mapped the owl localities on top of layers of summer temperature, precipitation, and vegetation (Latifovic et al. 2002) to assess support for the Barred Owl range expansion being constrained by the presence of coniferous forests (Boxall and Stepney 1982). For purposes of significance testing, and in an effort to reduce problems of non-independence associated with spatial autocorrelation of the data, we iteratively randomly sampled 50 Barred Owl localities (100,000 times) from the source and corridor polygons.

Distributions of owls in geographic and climatic space.—We characterized the distributions of Barred Owl, Spotted Owl, and Barred × Spotted owl hybrid offspring in both geographic and climatic space. Nineteen climate variables (Hijmans et al. 2005) broadly summarized temperature and precipitation means, as well as seasonal variability (Table 1). We used principal component analysis (PCA) on the climate data to identify three composite axes explained most of the total sample variation. Statistical significance of the component loadings was determined using a randomization procedure (10,000 iterations) with Bonferroni correction ($\alpha = 0.05/57$). We then used a second-order point process measure, the K function (Ripley 1976), to determine across different spatial scales whether the owl taxa were randomly or nonrandomly distributed within regions of parental overlap. We compared the K function of the observed number of owl occurrences within distance (d) of an arbitrary point of occurrence with the expected number of occurrences, here modeled as a random (Poisson) process where $K(d) = \pi d^2$. Values of K greater than πd^2 indicate higher observed densities than expected by chance (i.e., clustering), whereas K values less than πd^2 indicate lower observed densities than expected by chance (i.e., avoidance). Functions of K were computed using latitude and longitude and with the scores from the first three principal components. Geographic simulations were restricted to a minimum convex polygon encompassing all localities where Spotted and Barred owls occur in

TABLE 1. Climate variables used in the principal component (PC) analysis.

Variable	PC 1	PC 2	PC 3
Annual mean temperature	0.161	-0.943*	0.248
Mean diurnal temperature range	0.050	-0.028	0.788*
Isothermality	0.853*	-0.176	0.389
Temperature seasonality	-0.943*	0.183	-0.087
Maximum temperature of warmest month	-0.269	-0.764*	0.498
Minimum temperature of coldest month	0.698*	-0.671*	0.167
Temperature annual range	-0.903*	0.229	0.136
Mean temperature of wettest quarter	-0.535	-0.601*	0.014
Mean temperature of driest quarter	0.748*	-0.369	0.243
Mean temperature of warmest quarter	-0.335	-0.880*	0.227
Mean temperature of coldest quarter	0.595*	-0.757*	0.240
Annual precipitation	0.594*	-0.262	-0.704*
Precipitation of wettest month	0.825*	0.006	-0.450
Precipitation of driest month	-0.406	-0.614*	-0.557
Precipitation seasonality	0.698*	0.450	0.391
Precipitation of wettest quarter	0.822*	0.035	-0.460
Precipitation of driest quarter	-0.326	-0.636*	-0.601*
Precipitation of warmest quarter	-0.546	-0.607*	-0.412
Precipitation of coldest quarter	0.877*	0.087	-0.396

*Randomization test for significance of component loadings: $P < 0.05/57$.

sympatry (roughly 125–118.5°W and 37.5–51°N). Climate simulations were run for this same invaded region projected into principal-component space, as defined by all two-dimensional combinations of the first three composite axes, which explained 87% of the cumulative percentage trace. Analyses proceeded separately for Spotted, Barred, and hybrid owls, both before and after postnatal dispersal, with 1,000 iterations per simulation.

RESULTS

Historical climate change and the Barred Owl invasion.—North America experienced spatially heterogeneous changes in summer temperature and precipitation during the early to mid-20th century (Fig. 2A, B). Patterns of warming were particularly pronounced in the Barred Owl expansion corridor (Fig. 3A). Areas in the extreme north of the corridor warmed by more than 2°C. Temperature increases in the putative source areas were comparably small in magnitude (Fig. 3A). The mean change in summer temperature for the corridor (+1.1°C) was significantly greater than zero ($t = 2.8$, $df = 96$, $P < 0.05$), whereas the mean change for the source (+0.5°C) did not deviate significantly from zero ($t = 2.0$, $df = 96$, $P > 0.05$). Furthermore, the mean increase in summer temperature in the corridor was significantly greater than that in the source ($t = 8.8$, $df = 82$, $P < 0.001$). Hence, although both the corridor

and source localities had summer warming during the early to mid-20th century, the corridor warmed considerably more than the source. At the beginning of the 20th century, the source was 4.0°C warmer than the corridor, but by 1970, the temperature difference had decreased to 3.3°C. The temperature difference between the source in the first decade of the 20th century and the corridor around 1970 was 2.9°C. These warming trends were largely incremental from 1901 through 1970 (Fig. 4).

Contrary to the original hypothesis, both the corridor and source localities became drier during the early to mid-20th century (Fig. 3B). The mean change in summer precipitation for the source was significantly less than zero (-45 mm) ($t = -2.7$, $df = 83$, $P < 0.05$), whereas mean change for the corridor (-38 mm) did not deviate significantly from zero ($t = -1.3$, $df = 81$, $P > 0.05$). Furthermore, the mean decrease in summer precipitation in the corridor was not significantly different from that in the source ($t = 0.3$, $df = 88$, $P > 0.05$). Hence, the Barred Owl range expansion was not spatiotemporally concomitant with historical changes in summer precipitation.

Changes in climate also do not explain why the expansion corridor was positioned at such high latitudes (i.e., “cold” areas). Areas south of the corridor were warmer and would have afforded a more direct route to western North

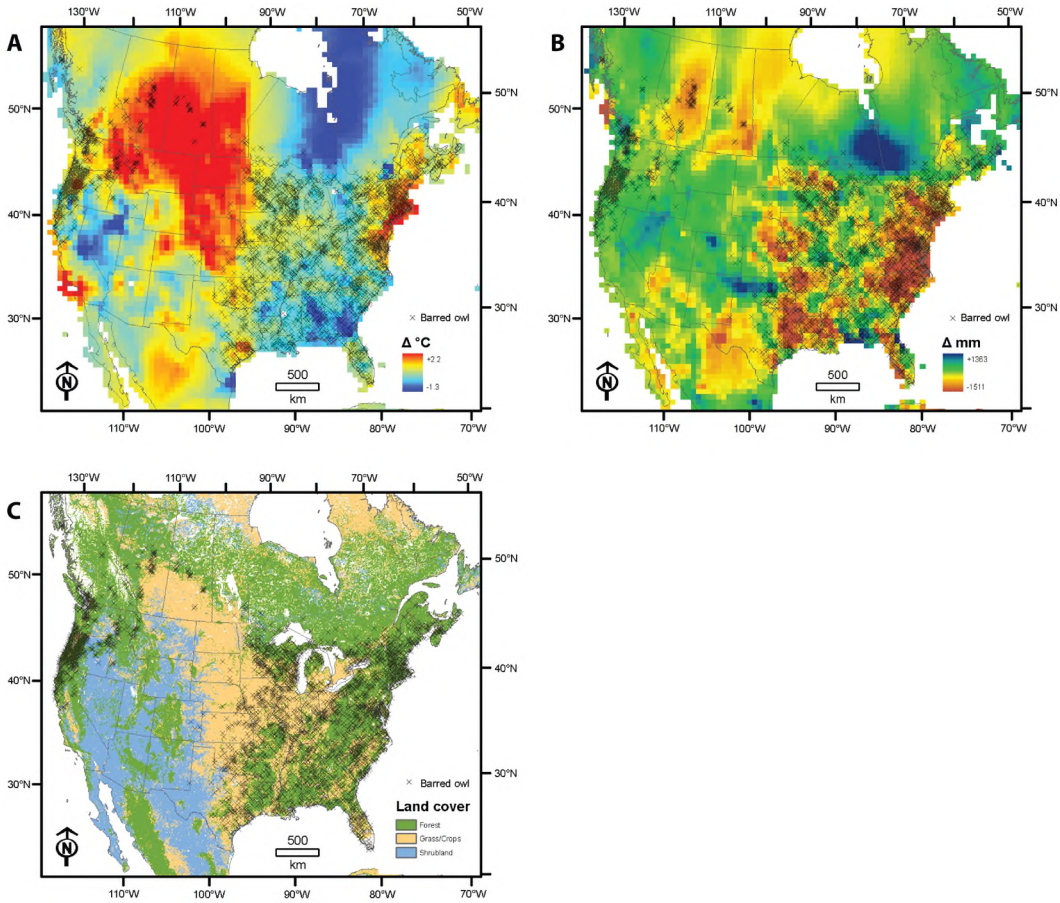


FIG. 2. Major environmental associations of the Barred Owl. (A) Change in mean summer temperature, mean(1961:1970) – mean(1901:1910). (B) Change in mean summer precipitation, mean(1961:1970) – mean(1901:1910). (C) Land cover classification derived from Latifovic et al. (2002). (Map projection: Albers equal-area conic.)

America. However, southern areas lacked the forested habitats that broadly characterize the core eastern range of the Barred Owl (Fig. 2C).

Geographic and climatic distributions of Barred, Spotted, and hybrid owls.—Principal component analysis simplified interpretation of the climatic associations of Barred, Spotted, and hybrid owls. The first three principal components accounted for most (87%) of the sample variation: 41% (PC 1), 28% (PC 2), and 18% (PC 3). The first principal component received especially large negative loadings from seasonal and annual measures of temperature variation (Table 1); PC 2 was characterized mostly by large negative temperature loadings; and PC 3 received large positive loadings from mean diurnal temperature range and large negative

loadings from annual precipitation and precipitation of the driest quarter.

The first two principal components captured distinct longitudinal gradients separating eastern Barred Owls from all western taxa (Fig. 5). Interpreting these components in light of the original variables, eastern Barred Owls occupied drier and climatically more variable environments than western owls. The second and third principal components failed to identify any additional groupings. Within invaded western regions, hybrids before and after postnatal dispersal were randomly distributed throughout areas of parental sympatry (Fig. 6A). Hybrids at both life stages were also randomly distributed throughout parental climate space as characterized by the first three principal components (Fig. 6B–D).

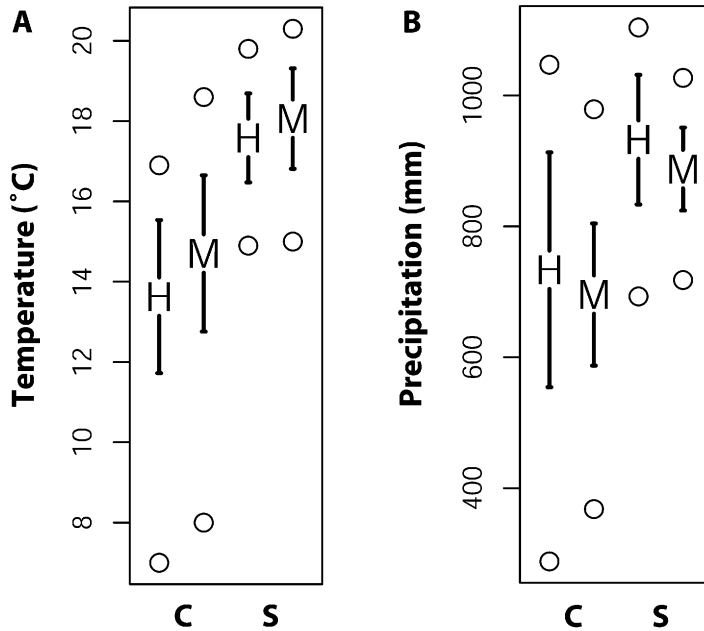


FIG. 3. Change in (A) mean summer temperature and (B) precipitation: Barred Owl expansion corridor (C; $n = 133$) vs. putative source (S; $n = 129$) localities (mean \pm 1 SD; open circles = extremes; H = "historical," 1901–1910; M = "modern," 1961–1970).

DISCUSSION

Our results confirm that the Barred Owl range expansion was concomitant with historical increases in mean summer temperature in the region, but not with changes in precipitation (Johnson 1994). Summer is a bioenergetically challenging season for the Barred Owl. Parents must continually provision offspring from spring hatching through late summer or early fall (Mazur and James 2000). Because metabolic energy requirements are inversely related to ambient temperature (Brown et al. 2004), the observation that the corridor warmed significantly more than the source shows that the two portions of the Barred Owl range became energetically more similar as the century progressed. Hence, climatically induced decreases in metabolic energy demand could explain in part how the Barred Owl was able to expand its range through such high latitudes and ultimately colonize western Spotted Owl habitats.

The fact that the expansion corridor traversed southern Canada, which despite summer warming remains colder than most other portions of the species' range, likely stems from habitat

restrictions. Boxall and Stepney (1982) speculated that there may have been a recent adaptation by the Barred Owl to coniferous forests. Adaptation or not, a more southern route would have had to traverse grassland and shrubland habitats that, in the absence of large trees with secondary cavities for nesting, are not considered suitable breeding habitats (Mazur and James 2000). In summary, the Barred Owl range expansion is best characterized as "natural" because (1) a distribution model accurately predicted the availability of western habitats where the species now occurs (Peterson and Robbins 2003), (2) the expansion corridor traversed forested areas that are largely representative of the core eastern range of the species, and (3) the timing of the expansion predated the clear onset of anthropogenically mediated climate warming—here taken to be about 1970, because temperature trends after this period cannot be explained by changes in solar radiation (Lean 1997).

Our results also show that juvenile and adult owl hybrids are randomly distributed both geographically and climatically with respect to Spotted and Barred Owl parentals, and that hybrids before and after postnatal dispersal

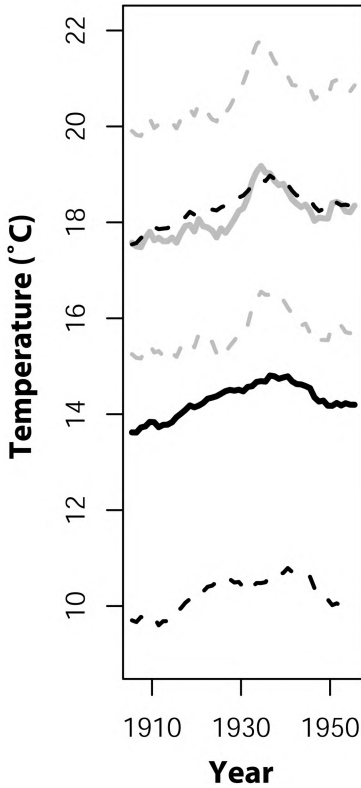


FIG. 4. Time series analysis of change in mean summer temperature (based on a 10-year moving window) in the Barred Owl expansion corridor (black) and in putative source (gray) localities. Solid lines indicate mean values; dashed lines show the 95% confidence intervals.

occupy similar geographic and climatic spaces. These findings suggest that owl hybrids have originated repeatedly in different environments and possess dispersal tendencies that favor parental backcrossing. The observation that hybrids can emerge at low frequencies throughout a large zone of parental overlap is significant, because it suggests opportunities for independent origins of recombinant genotypes in the very beginnings of hybrid establishment (Rieseberg 1997), which in turn increases the probability of transgressive characters arising and quickly becoming fixed (Buerkle et al. 2000). Following hybridization, dispersal can influence hybrid dynamics either by promoting the differential colonization of particular habitats or by ensuring random colonization of mostly parental environments. In the case of the owls, dispersal has allowed hybrids to remain randomly

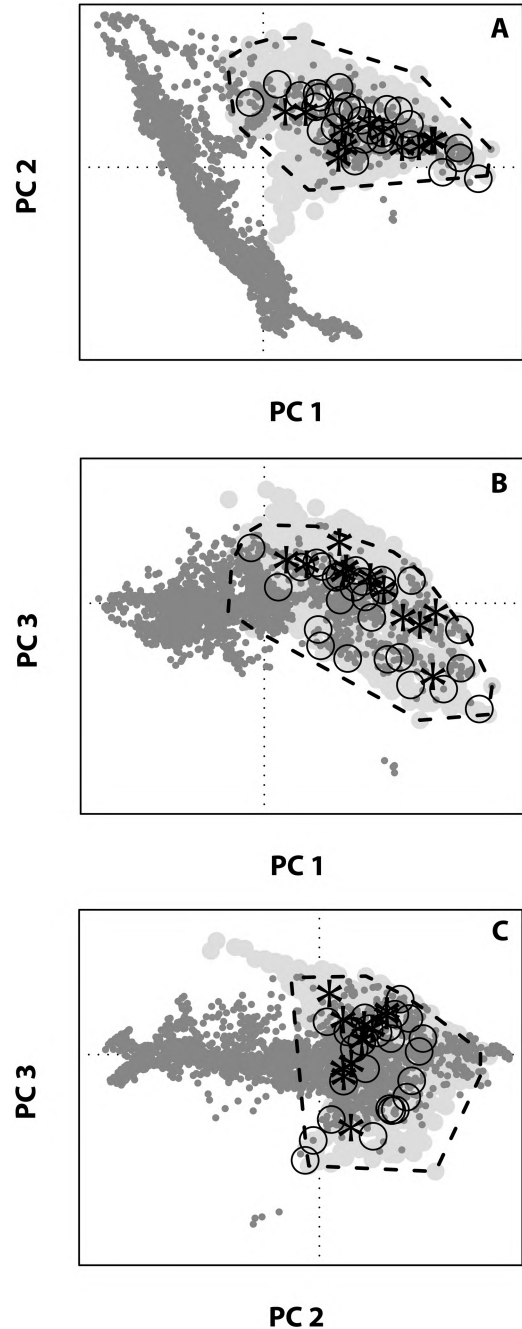


FIG. 5. Bivariate plots of component scores derived from PCA on climate variables. Dark gray points identify *S. varia*, light gray circles *S. occidentalis*, asterisks hybrids before postnatal dispersal, and open black circles hybrids after postnatal dispersal. Dashed black line delineates the invaded geographic space projected into component space.

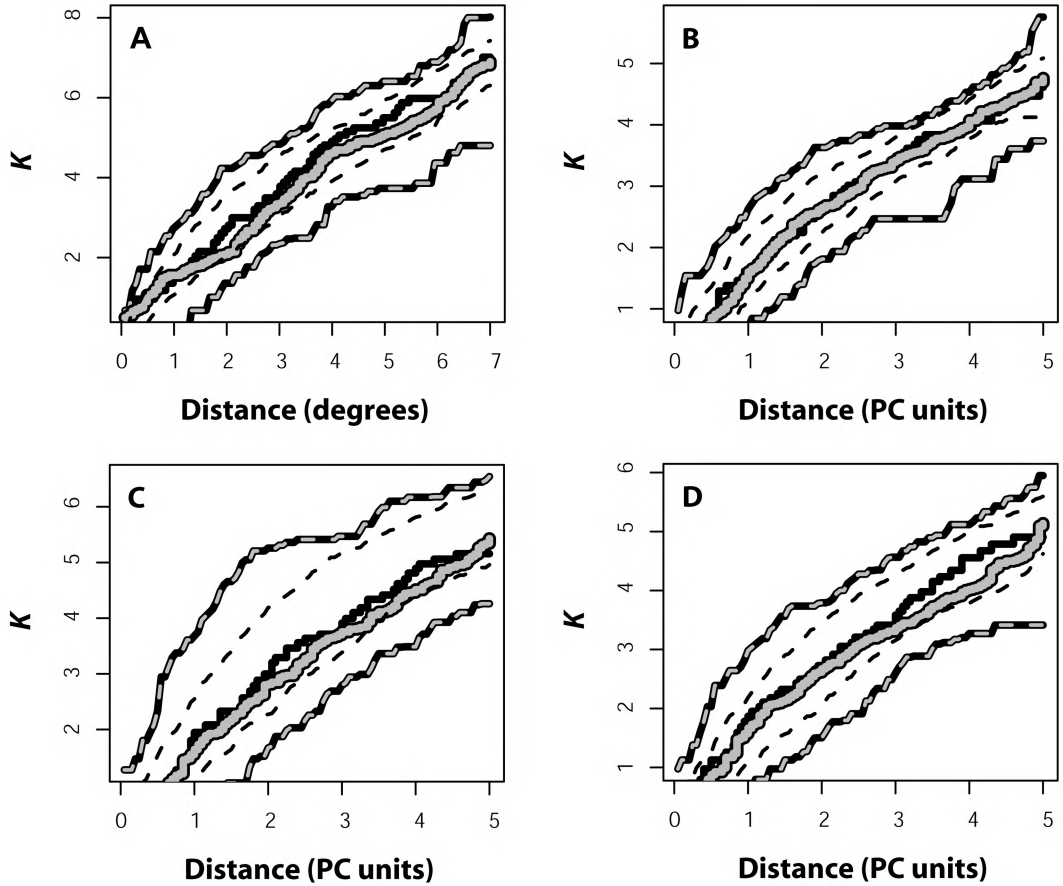


FIG. 6. Functions of K (Ripley 1976) describing distributions of hybrids before (gray; $n = 11$) and after (black; $n = 30$) postnatal dispersal (A) in invaded geographic space and (B–D) in multivariate climatic space as characterized by the first three principal components in the PCA: PC 2 vs. PC 1 (B), PC 3 vs. PC 1 (C), and PC 3 vs. PC 2 (D). Dashed lines identify minimum and maximum bounds of random expectations. Because in all cases the observed K values are bounded by the null K values, the results suggest that hybrid owls at both life stages are randomly distributed with respect to parentals.

distributed as breeding adults. However, because we were unable to follow individuals through development, what remains unknown is whether hybrids are tracking natal environments or truly dispersing randomly with respect to the geography and climate of the parentals.

Our results contribute two major points to the discussion of how hybridization should be considered in the context of conservation of *Strix* spp. First, the proximate origins of interspecific hybridization are, at large spatial scales, explained in part by climate and historical changes in climate. Because the Barred Owl range expansion tracked forested habitats and occurred during a period when warming trends

could be attributed to natural forces without invoking anthropogenic influences, we suggest that recent opportunities for Barred and Spotted owl hybridization stem in large part from natural processes. Second, Barred, Spotted, and first filial Barred \times Spotted owl hybrids are shown to exhibit high levels of geographic and niche overlap, at least as measured according to climate. This spatial arrangement promotes parental backcrossing over assortative hybrid mating. In such cases of weak niche or habitat differentiation, one taxon ultimately is expected to replace the other two (Wolf et al. 2001).

Given the recency of the Barred Owl invasion, conservation of *Strix* spp. in the short term will

still depend largely on whether critical Spotted Owl habitats continue to persist (Gutiérrez 1994, Gutiérrez et al. 1995). Because the issue of habitat availability is of fundamental conservation concern to all species, it is perhaps not surprising that most endangered-species legislation has focused more on mitigating threats posed by habitat loss than on addressing invasion and hybridization. However, the challenge posed by hybridization will need to be addressed increasingly in the coming decades, as climate change and other human-mediated invasions continue to pave the way for new species interactions (Mooney and Cleland 2001). Certainly, genetic approaches to identifying hybrid influences will be critical. We emphasize that spatial considerations of parentals and hybrids also can help predict future dynamics.

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