



The Auk 124(2):690–704, 2007
© The American Ornithologists' Union, 2007.
Printed in USA.

HIGH CONNECTIVITY AND MINIMAL GENETIC STRUCTURE AMONG NORTH AMERICAN BOREAL OWL (*AEGOLIUS FUNEREUS*) POPULATIONS, REGARDLESS OF HABITAT MATRIX

MARNI E. KOOPMAN,¹ GREGORY D. HAYWARD, AND DAVID B. McDONALD

Department of Zoology and Physiology, University of Wyoming, Laramie, Wyoming 82071, USA

ABSTRACT.—Habitat connectivity and corridors are often assumed to be critical for the persistence of patchily distributed populations, but empirical evidence for this assumption is scarce. We assessed the importance of connectivity among habitat patches for dispersal by a mature-forest obligate, the Boreal Owl (*Aegolius funereus*). Boreal Owls demonstrated a lack of genetic structure ($\theta = 0.004 \pm 0.002$ [SE]) among subpopulations, regardless of matrix type and extent, which indicates that unfor-ested matrix does not act as a barrier to dispersal for this vagile species. We found only slightly higher genetic distances (Cavalli-Sforza chord distances ranged from 0.015 to 0.025) among patchily distributed Rocky Mountain subpopulations as compared with largely contiguous boreal-forest subpopulations (0.013 to 0.019) and no evidence of a genetic split across the expansive high plains of Wyoming. Even the most isolated subalpine patches are connected via gene flow. As northern boreal forests continue to experience intensive harvest of mature stands, geographic dispersion of Boreal Owl habitat may begin to more closely resemble that found in the Rocky Mountains. We suggest that decreased connectivity poses much less of a threat to continued abundance of this mature-forest obligate than overall loss of nesting and foraging habitat. Assessment of the importance of corridors and connectivity should be conducted on a species-by-species basis, given the variation in response of species to discontinuity of habitat, even among closely related taxa or guilds. Received 5 October 2005, accepted 22 June 2006.

Key words: *Aegolius funereus*, Boreal Owl, connectivity, corridors, dispersal, gene flow, genetic structure, microsatellites.

Alta Conectividad y Estructura Genética Mínima entre Poblaciones Norteamericanas de *Aegolius funereus*, Independientemente de la Matriz del Hábitat

RESUMEN.—Frecuentemente, se supone que la conectividad del hábitat y los corredores son críticos para la persistencia de poblaciones distribuidas en parches, pero la evidencia empírica sobre esto es escasa. Evaluamos la importancia de la conectividad entre parches de hábitat para la dispersión en *Aegolius funereus*, una especie restringida a bosques maduros. Encontramos una ausencia de estructura genética entre subpoblaciones ($\theta = 0.004 \pm 0.002$ [EE]), independientemente del tipo de matriz y de su extensión, lo que sugiere que las matrices no boscosas no actúan como una barrera para la dispersión en esta especie de amplia movilidad. Sólo encontramos distancias genéticas ligeramente mayores (las distancias cuerda de Cavalli-Sforza estuvieron entre 0.015 y 0.025) entre subpoblaciones de las Montañas Rocallosas distribuidas en parches en comparación con subpoblaciones

¹Present address: Rocky Mountain Research Station, 240 West Prospect, Fort Collins, Colorado 80526, USA.
E-mail: marnikoopman@yahoo.com

de bosques boreales contiguos (0.013 a 0.019), y no observamos evidencia de una diferenciación genética a través de las amplias planicies altas de Wyoming. Incluso los parches subalpinos más aislados están conectados por flujo genético. A medida que los bosques boreales del norte continúen siendo sometidos a extracción intensiva de rodales maduros, la dispersión geográfica del hábitat de *A. funereus* en la región podría comenzar a semejarse más a la del hábitat de las Montañas Rocallosas. Sugerimos que la conectividad reducida representa una amenaza mucho menor sobre la abundancia de esta especie restringida a los bosques maduros que la pérdida general de hábitat de nidificación y forrajeo. Las evaluaciones de la importancia de los corredores y la conectividad deben realizarse especie por especie, dada la variación en la respuesta de las especies a la discontinuidad del hábitat, aún entre taxones estrechamente emparentados o pertenecientes al mismo gremio.

POPULATION BIOLOGISTS HAVE become increasingly interested in the spatial ecology of populations, with particular focus on dispersal as one of the fundamental processes influencing population dynamics (Walters 2000). Because of discontinuity of suitable habitat, most species exist in a patchy geographic distribution in all or part of their range, with dispersal among patches acting to connect the population as a whole. Dispersal influences species ranges, the synchrony of population fluctuations (Huitu et al. 2003), and long-term persistence of populations locally and range-wide (Levins 1969, Stacey and Taper 1992, Martin et al. 2000). Populations may experience less variation in abundance and higher persistence because of the exchange of individuals among patches that vary in productivity (Lande 1988). The idea that movement among subpopulations affects the persistence and dynamics of the broader population is central to the concept of metapopulations (Hanski 1999), but dispersal may be equally important in species that are not structured as a metapopulation.

Models and theoretical understanding indicate that the nature of the matrix (i.e., nonhabitat) between habitat patches can have far-reaching effects on populations (Gardner et al. 1991). Lower matrix quality and increased resistance may decrease the likelihood of population persistence (Fahrig 2001, Vandermeer and Carvajal 2001). Increased theoretical understanding of the effects of patchy spatial structure on such features as genetic diversity, dispersal rates, and extinction probabilities has led to management that often incorporates connectivity and corridors (Beier 1995, Dunning et al. 1995, Donnelly and Marzluff 2004), but

their efficacy suffers from a lack of empirical study (Simberloff et al. 1992, Rosenberg et al. 1997, Beier and Noss 1998, Berry et al. 2005), with the exception of a few well-documented cases (Beier 1993, Dunning et al. 1995, Mech and Hallett 2001). When dispersal through the matrix is sufficiently high, increased habitat connectivity may not increase population persistence or abundance (Hudgens and Haddad 2003), and limited conservation resources may be better spent preserving or improving available habitat rather than improving or maintaining connectivity. Additionally, some authors have suggested that habitat specialists are more sensitive to connectivity among habitat patches than habitat generalists (Rosenberg et al. 1997, Haddad 1999a), especially when large distances separate patches (Haddad 1999b). Understanding commonalities among guilds or taxa, levels of connectivity among subpopulations, and resulting relationships is critical to a thorough understanding of population dynamics with implications for management and conservation (Kareiva 1990).

Here, we explore the effects of habitat connectivity on movement among subpopulations of a mobile mature-forest obligate, the Boreal Owl (*Aegolius funereus*). Because of the geographic dispersion of suitable forest habitat, Boreal Owls exhibit two distinctive distribution patterns, which makes them attractive for investigating how connectivity affects dispersal rates. In northern boreal forests, Boreal Owls occur throughout highly connected habitat, but in subalpine forest farther south, Boreal Owls exist in isolated high-elevation patches separated by variable expanses of unsuitable matrix (Fig. 1; Hayward and Hayward 1993),

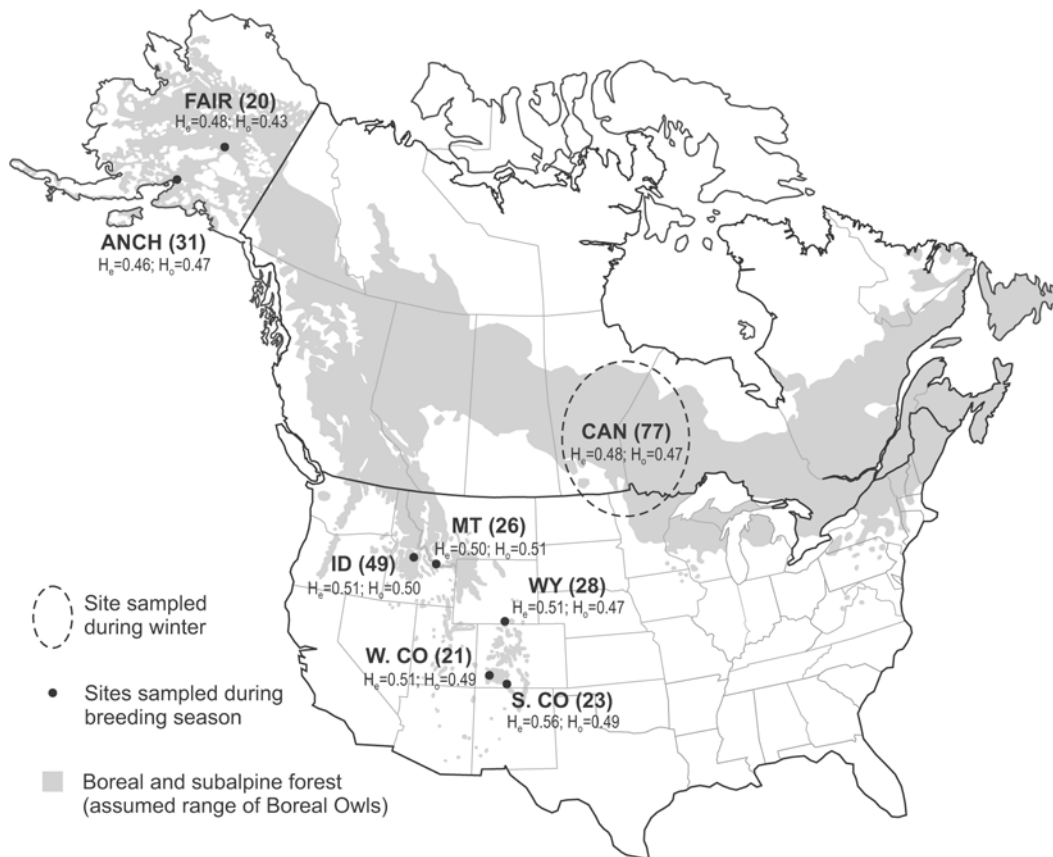


FIG. 1. The North American range of Boreal Owls, based on the distribution of boreal and subalpine forest. Sample sizes and expected and observed heterozygosities are listed for each sampling locality. Despite a potential metapopulation structure based on patchily distributed habitat in the Rocky Mountains of the United States, long-distance dispersal limits genetic differentiation among subpopulations.

including lower-elevation forest, prairie, desert, and urban development.

In addition to the contrasting patterns of dispersion, Boreal Owls in northern boreal forests and subalpine forests differ in ecology, behavior, and even basic life-history traits (Hayward 1997). Given their long dispersal distances and irruptive behavior in northern boreal forests (Löfgren et al. 1986, Korpimäki et al. 1987, Sonerud et al. 1988), Boreal Owls can be considered highly vagile. However, Boreal Owls have a Holarctic distribution (Hayward and Hayward 1993), and data on dispersal come from northern boreal forests in Fennoscandia. Subalpine populations in the Rocky Mountains of the United States are patchy, and barriers could prevent significant exchange among patches.

For example, the Northern Spotted Owl (*Strix occidentalis caurina*) requires corridors of mature forest to facilitate dispersal from one habitat patch to another (Miller 1989, Forsman et al. 2002). If Boreal Owls, which are also mature-forest obligates (Hayward 1997), required such dispersal corridors, we would expect a negative relationship between the extent of unforested matrix and gene flow.

Although dispersal is crucial for a variety of ecological functions, the difficulty associated with estimation of dispersal rates has contributed to poor understanding of this vital component of population ecology (Koenig et al. 1996, Walters 2000). We used microsatellite DNA markers to address the question of how matrix composition, including both type and extent,

affects movement among habitat patches. In contrast to direct methods such as radiotelemetry or satellite telemetry, genetic markers allow investigation into movement patterns of small animals at a continental scale. Furthermore, genetic approaches facilitate detection of relatively low movement rates that may not be detected by radiotelemetry or banding efforts. Molecular methods are not only becoming more economical than traditional field methods, they also may provide more informative data on dispersal, because only successful dispersers incorporate their genetic signature into the population (Koenig et al. 1996). With a variety of new statistical methods available to assess dispersal rates and patterns using molecular markers (Paetkau et al. 1995, Cornuet et al. 1999, Pritchard et al. 2000, Beerli and Felsenstein 2001, Goudet et al. 2002), biologists are discovering patterns of dispersal that were unexpected on the basis of field data alone (Scribner et al. 2001, Kerth et al. 2002, Korfanta et al. 2005).

We studied gene flow among subpopulations of Boreal Owls separated by a spectrum of matrix extent and type to determine the limits to dispersal by a vagile mature-forest obligate. Specifically, we hypothesized that patchy subpopulations in the Rocky Mountains, though geographically proximate, would show more genetic structure (higher F_{ST} values and genetic distances) than northern boreal-forest subpopulations that are geographically distant but highly connected. Because dispersal is a function of the extent and resistance of the matrix as well as the vagility of a species, we expected to find that forested matrix allowed more gene flow than unforested matrix. We hypothesized that the large expanse of high plains across Wyoming would act as a barrier to dispersal for Boreal Owls, as it has for a number of species of montane mammals (Findley and Anderson 1956). The genetic signature of such a barrier would appear as a departure from the null model of isolation-by-distance (genetic distance among subpopulations increasing linearly with geographic distance), resulting in a dramatic increase in genetic distance in the presence of inhospitable matrix (Paetkau et al. 1997).

We also expected that subpopulations of Boreal Owls in the Rocky Mountains would exhibit classical metapopulation structure. They fit many assumptions of the metapopulation concept, including discrete local populations

separated by inhospitable matrix and seemingly independent population dynamics. One assumption of the original metapopulation concept (Levins 1969) is that "the exchange rate of individuals among local populations is so low that migration has no real effect on local dynamics in the existing populations" (Hanski and Simberloff 1997:9). Given the extensive treeless matrix separating Rocky Mountain subpopulations, it seemed likely that dispersal (gene flow) would be limited, allowing subpopulation differentiation. Because much of metapopulation theory has developed with little empirical support from vertebrate studies, the potential to test metapopulation theory in such a system is very attractive, especially given that connected subpopulations in northern boreal forests allow for comparison to a baseline level of gene flow across largely continuous suitable breeding habitat.

METHODS

Sample collection and molecular genetic methods.—We sampled Boreal Owls in subpopulations separated by a spectrum of distances and matrix types (Table 1). By sampling the range of connectivity available to North American Boreal Owls, we were able to assess how matrix composition affects gene flow among subpopulations. We sampled birds at sites separated by habitat (boreal or subalpine forest), and by unsuitable matrix, including lower-elevation forest (e.g., ponderosa pine or Douglas fir), urban development, and treeless expanse (e.g., prairie, desert, shrublands). Here, we use the term "subpopulation" loosely, to refer to an area where we sampled Boreal Owls, rather than to a biological subpopulation.

Boreal Owls were captured primarily at nest boxes along logging roads on several national forests where an extensive system of nest boxes was established beginning in 1987 (Hayward et al. 1992). More than 2,000 nest boxes were checked each year, from 1998 to 2002. Samples from Idaho were collected between 1995 and 2002. On average, nest box use by Boreal Owls was only ~1%. Adult females were trapped while brooding or incubating, and males were trapped as they brought food to the chicks. We collected blood samples from all individuals captured. If we were unable to trap adults at a nest, we collected a blood sample from one of the nestlings.

TABLE 1. Pairwise comparisons of subpopulations of Boreal Owls in the boreal forest and in the Rocky Mountains showing the range of matrix types and geographic distances between subpopulations. We sampled subpopulations with varying types of dominant matrix between them, including suitable breeding habitat (boreal forest), montane forest (largely connected lower-elevation forest), patchy forest (disconnected subalpine and lower-elevation forest with interspersed grasslands), high plains, and urban development. Sample locations are shown in Figure 1.

Subpopulations being compared	Distance between subpopulations (km)	Dominant matrix types
W. CO / S. CO	166.6	Patchy forest
ID / MT	175.9	Montane forest
WY / W. CO	207.0	Patchy forest, urban development
WY / S. CO	368.6	Patchy forest, urban development
FAIR / ANCH	415.2	Boreal forest
MT / WY	781.6	High plains, patchy forest
MT / W. CO	881.3	High plains, patchy forest
ID / WY	893.7	High plains, patchy forest
ID / W. CO	961.8	High plains, patchy forest
MT / S. CO	1,020.2	High plains, patchy forest
ID / S. CO	1,083.8	High plains, patchy forest
FAIR / CAN	3,338.4	Boreal forest
ANCH / CAN	3,407.9	Boreal forest

Boreal Owls were tagged with a federal band so that we could recognize family members and recaptures. Tissue samples obtained from Boreal Owl specimens from Manitoba and Minnesota consisted of heart or muscle tissue. Additional tissue samples collected near Fairbanks, Alaska, were obtained from the University of Alaska museum. Blood was stored in Longmire's Solution (Longmire et al. 1988), and most tissue was stored in 100% ethanol.

To isolate DNA from samples, we used a Sigma GenElute mammalian DNA extraction kit (Sigma-Aldrich, St. Louis, Missouri). We genotyped 275 unrelated individuals using seven polymorphic microsatellite loci, following the protocol described by Koopman et al. (2004).

Genetic structure.—We assessed genetic structure of subpopulations of Boreal Owls in North America. Because microsatellite mutation processes are not fully understood at this time and there is no consensus on the most appropriate measurements to use (Goldstein and Pollock 1994, Ruzzante 1998, Foulley and Hill 1999, Kalinowski 2002), the use of a variety of measurements, with different underlying assumptions, can increase confidence in the results, especially if they agree (Neigel 2002). Some tests or measures assess differences among user-defined “subpopulations” (F_{ST} , measures of genetic distance), whereas

others assess differences (or similarities) among individuals, thereby allowing for identification of subpopulations based on genetic substructure (assignment tests, allele-sharing distances, model-based clustering method of the Bayesian program STRUCTURE).

We tested for departure from Hardy-Weinberg equilibrium, within and among each pair of loci, using GENEPOP, version 3.3 (Raymond and Rousset 1995) and, for genotypic linkage disequilibrium, FSTAT, version 2.9.3.2 (Goudet 1995). We used sequential Bonferroni procedures to adjust for multiple comparisons (overall $\alpha = 0.05$).

We estimated genetic differentiation among subpopulations, θ (equivalent to F_{ST}) using the measure of Weir and Cockerham (1984), which is weighted by sample size, in FSTAT. Ninety-five percent confidence intervals around Weir and Cockerham's F_{ST} (hereafter referred to simply as F_{ST}) were estimated with 10,000 bootstrap replicates. In GENEPOP, we ran a G-like exact test (Goudet et al. 1996) to assess differences among subpopulations in overall allelic distributions.

To evaluate the appropriate geographic scale for population-differentiation analysis, we used hierarchical F statistics (Weir 1996), which involve grouping of individual subpopulations,

on the basis of geographic proximity, until overall genetic differentiation is maximized. Using the grouping with highest genetic structure (greatest F_{ST}), we tested for genetic subdivision on a regional scale using a likelihood-based assignment test (Paetkau et al. 1995) in DOH (see Acknowledgments) and a Bayesian assignment test (Cornuet et al. 1999) in GENECLASS (see Acknowledgments). When populations show sufficient genetic differentiation ($F_{ST} > 0.05$; Cornuet et al. 1999), this procedure allows identification of individuals that may have dispersed between populations (Rannala and Mountain 1997). We also assessed structure among subpopulations or geographic regions using STRUCTURE (see Acknowledgments), which determines whether sampled genotypes are substructured into multiple ($K > 1$) clusters or whether they constitute a single genetically homogeneous population ($K = 1$) in Hardy-Weinberg equilibrium. We tested for one to eight separate subpopulations without prior information on capture location of individuals (Pritchard et al. 2000). Burn-in and replication values were set at 25,000 and 1,025,000.

Phylogenetic trees.—We calculated pairwise Cavalli-Sforza chord distances (Cavalli-Sforza and Edwards 1967) among subpopulations and generated a rooted neighbor-joining tree in the NEIGHBOR subroutine of PHYLIP (see Acknowledgments), with Norwegian Tengmalm's Owls (*A. f. funereus*) as an outgroup. Under microsatellite locus and sample number conditions similar to ours, chord distances show greater success in generating the correct tree topology than other distance measurements (Takezaki and Nei 1996). One-thousand bootstrap replications were performed to calculate percentage of support for individual nodes. A maximum-likelihood (ML) tree was also constructed using the ML subroutine (CONML) in PHYLIP and bootstrapped 1,000 times, with Tengmalm's Owls as an outgroup.

We calculated allele-sharing distances (Bowcock et al. 1994) using the MS TOOLS add-in for EXCEL (see Acknowledgments). Pairwise allele-sharing distances are calculated as one minus half the average number of shared alleles per locus. Finally, we constructed a neighbor-joining tree (Saitou and Nei 1987) in PHYLIP, using unrelated North American individuals as the operational taxonomic units.

Isolation-by-distance.—We compared matrices of pairwise genetic distance and pairwise

geographic distance using a Mantel test (Mantel 1967) and 5,000 permutations in MCMANTEL (McDonald et al. 1999). We calculated straight-line distances between subpopulations in ARCVIEW (ESRI, Redlands, California), using the center of the area where the most Boreal Owls were captured as the end points of each line connecting two subpopulations. Because most individuals were captured near Winnipeg for our samples from Canada, we used Winnipeg as the endpoint for our Canadian comparisons.

We hypothesized that, if matrix type regulates gene flow among subpopulations, we should see a departure from the linear isolation-by-distance model (Paetkau et al. 1997), such that subpopulations separated by inhospitable matrix would have higher genetic distance than expected from geographic distance alone.

We used three different pairwise measures of genetic distance. First, we calculated pairwise Cavalli-Sforza and Edwards (1967) chord distance because of its superior performance in phylogenetic tree-building (Takezaki and Nei 1996) and its linear nature over large distances, and because it makes no assumptions about mutation models. We also calculated the ratio $F_{ST}/(1 - F_{ST})$ (Rousset 1997) and Nei's standard distance (Nei 1972), both of which have been shown to accurately reflect isolation-by-distance (Takezaki and Nei 1996, Paetkau et al. 1997, Rousset 1997), though $F_{ST}/(1 - F_{ST})$ may be accurate only over small geographic distances (Rousset 1997). We decided not to use microsatellite-specific measurements because of departures from a strict stepwise mutation model (SMM) apparent in some of our loci and because other studies have found that the high variance associated with these measurements obscures patterns (Paetkau et al. 1997), especially with high levels of gene flow (Balloux and Goudet 2002).

RESULTS

The 275 genotyped individuals were from eight subpopulations (Fig. 1). The number of alleles per locus ranged from 3 to 11 among seven microsatellite loci. We found evidence for heterozygote deficiency at one locus in the subpopulation from Canada ($P < 0.001$). Otherwise, all subpopulations were in Hardy-Weinberg equilibrium for all loci. We found no evidence for genotypic disequilibrium among paired loci

(P values ranged from 0.01 to 0.96; adjusted 5% nominal level for multiple comparisons = 0.0025).

Genetic structure.—Genetic differentiation among subpopulations of Boreal Owls throughout North America was extremely small, as demonstrated by estimates of global F_{ST} ($\theta = 0.004 \pm 0.002$ [SE]; 95% CI: 0.000 to 0.008). We found no significant overall difference in allelic distribution among subpopulations (G -like test, $P = 0.794$, $df = 14$). Using STRUCTURE, we consistently found a higher log likelihood of one subpopulation ($-3,801.3$) rather than two to eight subpopulations ($-4,004.2$ to $-6,699.1$), which indicates that, throughout the North American range, Boreal Owls occur as a single genetically homogeneous population.

When we grouped all northern (Alaska and Canada) and southern (Colorado and Wyoming) subpopulations while excluding central subpopulations (Montana and Idaho), slightly more genetic structure was apparent. The magnitude of this structure, however, was still very small ($\theta = 0.012 \pm 0.003$ [SE]; 95% CI: 0.007 to 0.017). We conducted the assignment test by reclassifying our samples into two groups: north and south, excluding Idaho and Montana. However, regardless of assignment algorithm, few individuals were correctly assigned to their origin of capture, because of low levels of genetic differentiation between northern and southern subpopulations (Fig. 2). When we used the assignment test of Paetkau et al. (1995), only 65% of individuals (133 of 206) were correctly assigned to their sampled subpopulation. On the basis of chance alone, one would expect 50% of individuals to be correctly assigned. Under the Bayesian method of Cornuet et al. (1999), only one individual of 206 had a significantly higher likelihood of having originated in the subpopulation from which it was sampled than in the other subpopulation.

Phylogenetic trees.—A phylogenetic tree for the eight North American subpopulations recovered the geographic split between northern and southern subpopulations of Boreal Owls (Fig. 3), but bootstrap support for most clades was extremely low. Rocky Mountain subdivisions had higher bootstrap support than other clades. Results from the ML tree corroborated those from the neighbor-joining tree. Our neighbor-joining tree of allele-sharing distances between individuals showed no clustering based on capture location (Fig. 4).

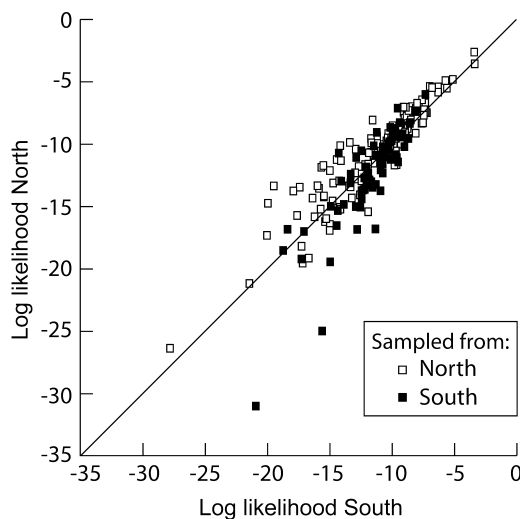


FIG. 2. Assignment likelihoods for 206 individuals captured in northern (Alaska and Canada) and southern (Colorado and Wyoming) subpopulations of Boreal Owls. If genotype were a good indicator of origin, most individuals from the north would have fallen well above the line, whereas those from the south would have fallen well below the line. The obvious lack of pattern and proximity to the line of equal likelihood both suggest a lack of clear genetic differentiation.

Isolation-by-distance.—Cavalli-Sforza chord distances were extremely small, ranging from 0.013 to 0.019 among boreal forest subpopulations and 0.015 to 0.025 among Rocky Mountain subpopulations. Similarly, Nei's standard distances ranged from 0.006 to 0.020 among boreal forest subpopulations and from 0.006 to 0.030 among Rocky Mountain subpopulations. Pairwise comparisons of geographic distance among all subpopulations were significantly correlated with Cavalli-Sforza chord distances ($R = 0.559$, $P = 0.001$), but not with $F_{ST}/(1 - F_{ST})$ ($R = 0.143$, $P = 0.238$) or Nei's standard distance ($R = 0.116$, $P = 0.280$). By contrast, all three genetic distances were significantly correlated with geographic distances when we assessed only the Rocky Mountain subpopulations (R ranged from 0.752 to 0.847; $P < 0.008$; Fig. 5). Nei's standard genetic distance had the best fit, but the relationship was confounded by the fact that larger distances between subpopulations in the Rockies were correlated with treeless matrix (Fig. 5).

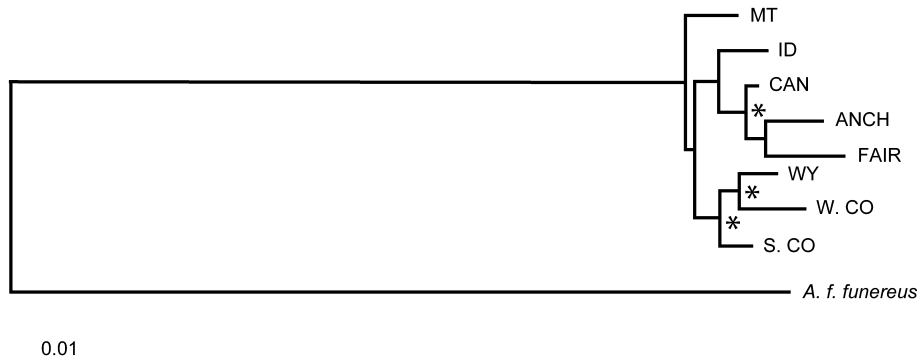


FIG. 3. Neighbor-joining tree of Cavalli-Sforza chord distances among subpopulations of North American Boreal Owls, with the Norwegian subspecies included as an outgroup. Percentage of support for each node was calculated from 1,000 trees built from bootstrapped data. Nodes with >50% support (marked with an asterisk) include the node joining Canada, Anchorage, and Fairbanks (54% support); that joining western Colorado, southern Colorado, and Wyoming (66%); and that joining western Colorado and Wyoming (69%). Higher bootstrap support for southern Rocky Mountain clades may indicate slightly less gene flow because of patchy habitat.

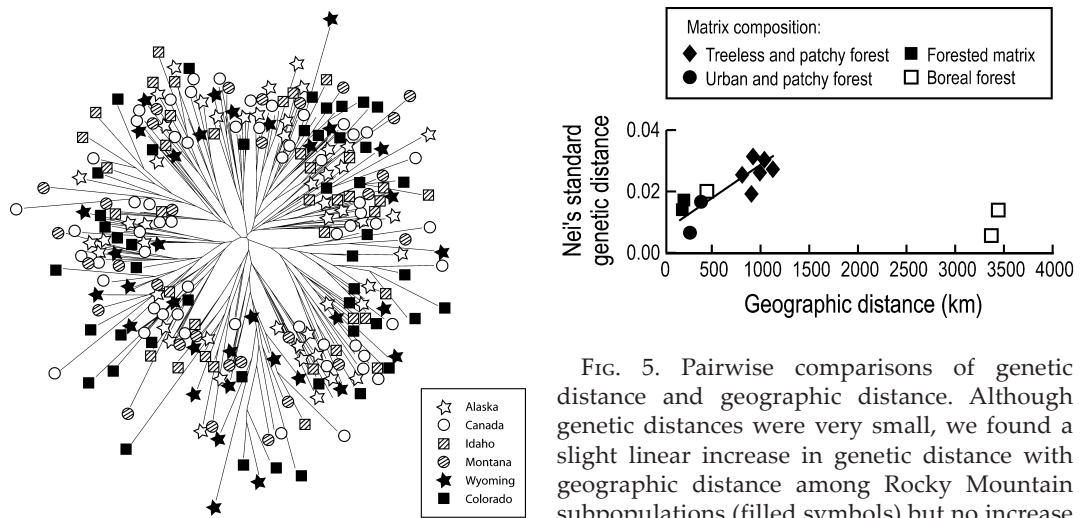


FIG. 4. Unrooted neighbor-joining tree of allele-sharing distances among 250 unrelated Boreal Owls captured in North America. If subpopulations were genetically well differentiated, individuals sampled from the same locality would cluster together. The obvious lack of clustering indicates a lack of genetic structure among Boreal Owl subpopulations in North America. By contrast, including Old World subpopulations produces nearly total reciprocal monophyly among Old World and New World populations, even when using individuals as the operational taxonomic units (Koopman et al. 2005).

FIG. 5. Pairwise comparisons of genetic distance and geographic distance. Although genetic distances were very small, we found a slight linear increase in genetic distance with geographic distance among Rocky Mountain subpopulations (filled symbols) but no increase among subpopulations separated by boreal-forest habitat (open squares). Although the slope of the line appears to be quite steep, the total change in genetic distance is only 0.03; for other published studies, Nei's distances may be an order of magnitude higher (McDonald et al. 1999). The relationship between geographic distance and genetic distance was confounded by matrix type in the Rocky Mountains, where treeless matrix was associated with longer distances; but even across treeless matrix, genetic distances were very small.

DISCUSSION

Many species exhibit naturally patchy distributions, and even more are becoming patchily distributed because of habitat loss. Resource managers require improved understanding of dispersal, resulting spatial patterns, and relationships to population persistence and demography. Empirical evidence for the efficacy of connectivity and corridors is scarce, but a few cases clearly demonstrate the importance of connectivity and favorable matrix in facilitating dispersal among habitat patches (Beier 1993, Dunning et al. 1995, Berry et al. 2005). Boreal Owls, on the other hand, exhibit only a modest increase in genetic structure when habitat patches are more isolated (Fig. 3). Dispersal rates are high even when patches are separated by inhospitable matrix, long distances, or both. Given their dependence on mature forest for foraging and nesting (Hayward 1997), we expected that Boreal Owls would require continuity of forested habitat to traverse the matrix. Our results reveal that generalizations about movement rates based on closely related taxa (e.g., Spotted Owls) or guilds (e.g., mature-forest obligates) are not reliable, and that assessment of the benefits of connectivity needs to be done on a species-by-species basis. If dispersal rates among subpopulations are high, managing matrix composition for connectivity among subpopulations may waste scarce conservation resources.

Are Boreal Owls a metapopulation?—With an F_{ST} of 0.004, Boreal Owls in North America are not partitioned into distinct subpopulations. Despite the patchy distribution of spruce–fir forest throughout the Rocky Mountains and despite strong dependence of Boreal Owls on mature forest, our genetic analysis indicates that Boreal Owl subpopulations do not constitute a metapopulation. High rates of gene flow among subpopulations of Boreal Owls make it unlikely that local populations exhibit independent population dynamics or that recruitment is almost invariably local, some of the fundamental tenets of classical metapopulation theory (Harrison and Taylor 1997). Various measurements (both classic ones, such as F_{ST} and Nei's standard distance, as well as more recently developed Bayesian and likelihood-based measurements) painted similar pictures of lack of distinct genetic structure among subpopulations. A lack of genetic structure among subpopulations indicates that this resident but highly vagile owl

frequently disperses long distances over inhospitable habitat, even >200 km across the high plains of Wyoming. We caution against applying the term "metapopulation" on the basis of physical patchiness of habitat only (Major et al. 1999, Martin et al. 2000, Sweanor et al. 2000).

Boreal Owls have extremely large home ranges for birds their size (Hayward et al. 1993), and in boreal forest, they are known to move great distances during natal dispersal and winter irruptions (Löfgren et al. 1986, Korpimäki et al. 1987). In addition, females find new mates each year, sometimes in new home ranges (Hayward et al. 1993). Over their lifetimes, total area traversed may span hundreds to thousands of square kilometers.

Habitat connectivity and Boreal Owls.—Genetic distances among sites with forested and treeless matrix differed minimally, leading us to conclude that dispersal rates are high, regardless of matrix type and extent. In the Rocky Mountains, all three measures of genetic distance increased linearly, if slightly, with geographic distance, as expected under the island model with no barriers to dispersal (Fig. 5). However, greater distances between Rocky Mountain subpopulations were correlated with treeless matrix, making it difficult to determine whether matrix type or distance was the primary factor involved in the significant relationship. In either case, gene flow was sufficiently high, even between the most distant and disconnected patches, to homogenize subpopulations genetically. For example, the assignment test failed to assign individuals to their population of origin, STRUCTURE indicated that Boreal Owls constitute a single population, and the individual-based neighbor-joining tree (Fig. 4) showed total lack of clustering of individuals sampled at the same locale.

Our results demonstrate that Boreal Owls disperse across large areas of unsuitable habitat and that no North American subpopulation is genetically isolated from the others. These high rates of gene flow make it unlikely that subpopulations are demographically independent. High dispersal rates likely act to dampen population fluctuations and boost breeding success in population sinks (the "rescue effect"; Brown and Kodric-Brown 1977), synchronize demographic patterns among subpopulations (Huitu et al. 2003), and overwhelm adaptations to local conditions. Some subpopulations

in the Rocky Mountains are less productive than others (M. E. Koopman unpubl. data) and may depend on high levels of immigration for long-term persistence. Nevertheless, the time-scale of genetic homogenization (on the order of several to many generations) may overlook demographic patterns that occur on a much shorter scale of a few years. Although genetic substructuring clearly suggests demographic independence among subpopulations, a lack of genetic structure does not necessarily preclude a degree of demographic independence. Thus, the relationship between gene flow and demographic patterns invites further investigation.

Boreal vs. subalpine subpopulations.—Differences in climate, habitat structure, prey cycles, and prey composition between northern boreal forests and more southerly subalpine forests appear to drive behavioral and ecological differences between northern and southern subpopulations of Boreal Owls (Hayward 1997). Judging from these differences in broad-scale dynamics, we expected high connectivity in the north and classical metapopulation structure in the southern parts of the range. We found slightly lower values of genetic distance among widely separated boreal-forest subpopulations than among proximate Rocky Mountain subpopulations (Fig. 5), which indicates that patchiness of habitat may slow movement. Similarly, we found higher bootstrap support for subdivisions among Rocky Mountain subpopulations than for subdivisions among northern subpopulations in our neighbor-joining and ML trees. The differences in genetic distance were slight, however, and were overshadowed by a consistent lack of genetic structure under global F_{ST} , assignment tests, a G -like test, STRUCTURE, and allele-sharing distances.

Our boreal-forest samples were from two breeding subpopulations in Alaska, plus irruptive individuals in northern Minnesota and southern Manitoba (labeled "CAN" in Fig. 1). Our samples from Canada represented individuals that moved south from a wider breeding range farther north because of severe winter conditions. No genetic differentiation existed between our samples from Alaska and Canada, and we feel confident that this is representative across the boreal forest of North America. Similarly, no genetic differentiation existed among Boreal Owls sampled in far eastern and far western locations in the Eurasian boreal

forest (Koopman et al. 2005). By contrast, Old World and New World populations showed a high degree of differentiation ($\theta = 0.37$; Koopman et al. 2005), demonstrating that a threshold level exists, at least at intercontinental scales.

Genetic differentiation.—The level of genetic differentiation in our study ($\theta = 0.004$) was lower than that found, using microsatellite markers, among subpopulations of other avian species (0.027 for Greater Sage-Grouse [*Centrocercus urophasianus*], Oyler-McCance et al. 1999; 0.014 for Yellow Warbler [*Dendroica petechia*], Gibbs et al. 2000; 0.014 for Burrowing Owl [*Athene cunicularia*], Korfanta 2001; 0.02 for Song Sparrow [*Melospiza melodia*], Chan and Arcese 2002), especially considering that our study was conducted over a larger spatial extent than most of the others. Even though genetic distances were small, we found evidence of limited genetic subdivision in the neighbor-joining and ML trees, which revealed two clades among North American Boreal Owls. The southern clade showed >50% support for subdivisions in Colorado and Wyoming. Hierarchical F statistics lent support to the north versus south split, with Montana and Idaho acting as middle ground between the two clades. The fact that slight genetic subdivision is apparent only at a continent-wide scale does not support our hypothesis that the treeless sagebrush steppe of the Wyoming Basin acts as a physical barrier to dispersal for Boreal Owls. By contrast, many mammalian spruce-fir forest obligates have distinct northern and southeastern subspecies or are limited in their range by the Wyoming Basin (Findley and Anderson 1956).

Boreal-forest subpopulations of Boreal Owls undergo irruptions, or mass southward movements of individuals, during extreme conditions (Hayward and Hayward 1993). Subalpine subpopulations in the Rocky Mountains do not, possibly explaining their slightly greater genetic differentiation. Winter irruptions may drive waves of immigrants from northern boreal forests into southern subalpine forests, thereby largely overwhelming any local adaptations or genetic structuring.

Implications for Boreal Owl management in subalpine and boreal forests.—Breeding populations of Boreal Owls throughout inland mountain ranges of the western United States were not detected until the mid- to late 1980s (Hayward

et al. 1987). Since then, Boreal Owls have been regarded as isolated mountain-top dwellers that are rarely heard or seen. Subpopulations are often managed at the geographic scale of individual national forests, and local subpopulations likely remain undiscovered in certain regions. The response of Boreal Owls to forest-management practices and large-scale habitat alterations is, therefore, virtually unknown.

In light of earlier understanding, the present study provides managers with a more optimistic scenario for long-term persistence of Boreal Owls, especially in the Rocky Mountains, where individual subpopulations are smaller and potentially more vulnerable to extinction. Because Boreal Owls appear to be structured not as a metapopulation, but instead as a well-connected yet patchily distributed population, consideration of connectivity and matrix composition is not as critical for management as it would be under a classic metapopulation structure. Additionally, temporary extinctions of local populations resulting from large-scale natural disturbances and extensive timber harvest, both of which we have observed (M. E. Koopman et al. unpubl. data), are likely to be followed by recolonization when mature spruce–fir habitat is restored, even when the nearest extant subpopulation is distant or separated by treeless matrix. With this knowledge, managers can focus conservation resources on other aspects of Boreal Owl life history, such as managing large tracts of mature spruce–fir forest habitat to sustain foraging and nesting requirements (Hayward 1997).

We have referred to the northern boreal forest as a large swath of connected habitat hospitable to Boreal Owls. Indeed, Boreal Owls are quite numerous throughout the region. Because of intensive logging pressure in the boreal forest, however, Boreal Owls in this region may begin to more closely resemble Rocky Mountain subpopulations as large tracts of habitat are lost and remaining tracts become disconnected. On a positive note, discontinuity of boreal forest may not significantly increase extinction probabilities because of high rates of dispersal among suitable habitat patches, as long as sufficient tracts of mature forest continue to persist on the landscape. We acknowledge, however, that a decrease in connectivity is only one of many deleterious effects of habitat fragmentation. Influx of invasive species, disease, competitors,

and predators (Brittingham and Temple 1983, Wilcove 1985, Burke and Nol 1998, Brown and Sullivan 2005) can act to degrade remaining habitat patches and negatively affect mature-forest obligates such as Boreal Owls. Although Boreal Owls are currently numerous across much of their range, and their ability to disperse across inhospitable matrix increases their probability of persistence, their close ties to a quickly vanishing habitat type continues to represent a significant threat to the future abundance of this species.

ACKNOWLEDGMENTS

More U.S. Forest Service (USFS) biologists than we can name here provided logistical support in the field—thanks to all of them, especially F. Gordon, C. Hescok, S. Jacobson, J. Ormiston, and R. Skorkowsky. We are grateful to T. Bodreaux, B. Dittrick, T. Holland, L. Moorehead, T. Swem, E. Taylor, and especially C. Schultz, for generously sending samples from Boreal Owls. Additional Boreal Owl genetic samples were provided by the Bell Museum, the Agricultural University of Norway, Manitoba Conservation, University of Alaska Museum, and the Burke Museum. We had excellent field assistance by many dedicated biologists, including L. Ayers, J. Bassinger, J. Bennett, J. Carpenedo, S. Dubay, T. Hampton, the Hayward family, T. Heekin, K. Keffer, S. Koopman, S. Mullins, K. Ott, M. Suedkamp, and P. Sutherland. J. Bennett provided GIS support. This project was funded by Global Forest (GF-18-2000-132), USFS Rocky Mountain Research Station, the Nansen Endowment (grant to G. A. Sonnerud), and awards from the American Museum of Natural History, Sigma Xi, and the Department of Zoology and Physiology and the Institute of Environment and Natural Resources at the University of Wyoming. Insight and ideas provided by S. Jackson, J. Lovvorn, and S. Anderson are greatly appreciated. The comments of G. A. Sonnerud and an anonymous reviewer greatly enhanced this manuscript. The DOH assignment test calculator is available at www2.biology.ualberta.ca/jbrzusto/Doh.php, GENECLASS at www.montpellier.inra.fr/URLB/geneclass/geneclasse.html, PHYLIP at evolution.genetics.washington.edu/phylip.html, the MS TOOLS add-in for EXCEL at animalgenomics.ucd.ie/sdepart/ms-toolkit/, and STRUCTURE at pritch.bsd.uchicago.edu/.

LITERATURE CITED

- BALLOUX, F., AND J. GOUDET. 2002. Statistical properties of population differentiation estimators under stepwise mutation in a finite island model. *Molecular Ecology* 11: 771–783.
- BEERLI, P., AND J. FELSENSTEIN. 2001. Maximum likelihood estimation of a migration matrix and effective population sizes in n subpopulations by using a coalescent approach. *Proceedings of the National Academy of Sciences USA* 98:4563–4568.
- BEIER, P. 1993. Determining minimum habitat areas and habitat corridors for cougars. *Conservation Biology* 7:94–108.
- BEIER, P. 1995. Dispersal of juvenile cougars in fragmented habitat. *Journal of Wildlife Management* 59:228–237.
- BEIER, P., AND R. F. NOSS. 1998. Do habitat corridors provide connectivity? *Conservation Biology* 12:1241–1252.
- BERRY, O., M. D. TOCHER, D. M. GLEESON, AND S. D. SARRE. 2005. Effect of vegetation matrix on animal dispersal: Genetic evidence from a study of endangered skinks. *Conservation Biology* 19:855–864.
- BOWCOCK, A. M., A. RUIZ-LINARES, J. TOMFOHRDE, E. MINCH, J. R. KIDD, AND L. L. CAVALLI-SFORZA. 1994. High resolution of human evolutionary trees with polymorphic microsatellites. *Nature* 368:455–457.
- BRITTINGHAM, M. C., AND S. A. TEMPLE. 1983. Have cowbirds caused forest songbirds to decline? *BioScience* 33:31–35.
- BROWN, J. H., AND A. KODRIC-BROWN. 1977. Turnover rates in insular biogeography: Effect of immigration on extinction. *Ecology* 58:445–449.
- BROWN, W. P., AND P. J. SULLIVAN. 2005. Avian community composition in isolated forest fragments: A conceptual revision. *Oikos* 111:1–8.
- BURKE, D. M., AND E. NOL. 1998. Influence of food abundance, nest-site habitat, and forest fragmentation on breeding Ovenbirds. *Auk* 115:96–104.
- CAVALLI-SFORZA, L. L., AND A. W. F. EDWARDS. 1967. Phylogenetic analysis: Models and estimation procedures. *American Journal of Human Genetics* 19:233–257.
- CHAN, Y., AND P. ARCESE. 2002. Subspecific differentiation and conservation of Song Sparrows (*Melospiza melodia*) in the San Francisco Bay region inferred by microsatellite loci analysis. *Auk* 119:641–657.
- CORNUET, J.-M., S. PIRY, G. LUIKART, A. ESTOUP, AND M. SOLIGNAC. 1999. New methods employing multilocus genotypes to select or exclude populations as origins of individuals. *Genetics* 153:1989–2000.
- DONNELLY, R., AND J. M. MARZLUFF. 2004. Importance of reserve size and landscape context to urban bird conservation. *Conservation Biology* 18:733–745.
- DUNNING, J. B., JR., R. BORGELLA, JR., K. CLEMENTS, AND G. K. MEFFE. 1995. Patch isolation, corridor effects, and colonization by a resident sparrow in a managed pine woodland. *Conservation Biology* 9:542–550.
- FAHRIG, L. 2001. How much habitat is enough? *Biological Conservation* 100:65–74.
- FINDLEY, J. S., AND S. ANDERSON. 1956. Zoogeography of the montane mammals of Colorado. *Journal of Mammalogy* 37:80–82.
- FORSMAN, E. D., R. G. ANTHONY, J. A. REID, P. J. LOSCHL, S. G. SOVERN, M. TAYLOR, B. L. BISWELL, A. ELLINGSON, E. C. MESLOW, G. S. MILLER, AND OTHERS. 2002. Natal and breeding dispersal of Northern Spotted Owls. *Wildlife Monographs*, no. 149.
- FOULLEY, J.-L., AND W. G. HILL. 1999. On the precision of estimation of genetic distance. *Genetics, Selection, Evolution* 31:457–464.
- GARDNER, R. H., M. G. TURNER, R. V. O'NEILL, AND S. LAVOREL. 1991. Simulation of the scale-dependent effects of landscape boundaries on species persistence and dispersal. Pages 76–89 in *Ecotones: The Role of Landscape Boundaries in the Management and Restoration of Changing Environments* (M. M. Holland, P. G. Risser, and R. J. Naiman, Eds.). Chapman and Hall, New York.
- GIBBS, H. L., R. J. G. DAWSON, AND K. A. HOBSON. 2000. Limited differentiation in microsatellite DNA variation among northern populations of the Yellow Warbler: Evidence for male-biased gene flow? *Molecular Ecology* 9:2137–2147.
- GOLDSTEIN, D. B., AND D. D. POLLOCK. 1994. Least squares estimation of molecular distance—Noise abatement in phylogenetic reconstruction. *Theoretical Population Biology* 45:219–226.
- GOUDET, J. 1995. FSTAT (version 1.2): A computer program to calculate F -statistics. *Journal of Heredity* 86:485–486.

- GOUDET, J., N. PERRIN, AND P. WASER. 2002. Tests for sex-biased dispersal using bi-parentally inherited genetic markers. *Molecular Ecology* 11:1103–1114.
- GOUDET, J., M. RAYMOND, T. DE MEEÛS, AND F. ROUSSET. 1996. Testing differentiation in diploid populations. *Genetics* 144:1933–1940.
- HADDAD, N. M. 1999a. Corridor use predicted from behaviors at habitat boundaries. *American Naturalist* 153:215–227.
- HADDAD, N. M. 1999b. Corridor and distance effects on interpatch movements: A landscape experiment with butterflies. *Ecological Applications* 9:612–622.
- HANSKI, I. 1999. *Metapopulation Ecology*. Oxford University Press, United Kingdom.
- HANSKI, I. A., AND D. SIMBERLOFF. 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. Pages 5–26 in *Metapopulation Biology: Ecology, Genetics, and Evolution* (I. A. Hanski and M. E. Gilpin, Eds.). Academic Press, San Diego, California.
- HARRISON, S., AND A. D. TAYLOR. 1997. Empirical evidence for metapopulation dynamics. Pages 27–42 in *Metapopulation Biology: Ecology, Genetics, and Evolution* (I. A. Hanski and M. E. Gilpin, Eds.). Academic Press, San Diego, California.
- HAYWARD, G. D. 1997. Forest management and conservation of Boreal Owls in North America. *Journal of Raptor Research* 31:114–124.
- HAYWARD, G. D., AND P. H. HAYWARD. 1993. Boreal Owl (*Aegolius funereus*). In *The Birds of North America*, no. 63 (A. Poole, P. Stettenheim, and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.
- HAYWARD, G. D., P. H. HAYWARD, AND E. O. GARTON. 1993. Ecology of Boreal Owls in the northern Rocky Mountains, USA. *Wildlife Monographs*, no. 124.
- HAYWARD, G. D., P. H. HAYWARD, E. O. GARTON, AND R. ESCANO. 1987. Revised breeding distribution of the Boreal Owl in the northern Rocky Mountains. *Condor* 89:431–432.
- HAYWARD, G. D., R. K. STEINHORST, AND P. H. HAYWARD. 1992. Monitoring Boreal Owl populations with nest boxes: Sample size and cost. *Journal of Wildlife Management* 56:777–785.
- HUDGENS, B. R., AND N. M. HADDAD. 2003. Predicting which species will benefit from corridors in fragmented landscapes from population growth models. *American Naturalist* 161:808–820.
- HUITU, O., K. NORRDAHL, AND E. KORPIMÄKI. 2003. Landscape effects on temporal and spatial properties of vole population fluctuations. *Oecologia* 135:209–220.
- KALINOWSKI, S. T. 2002. Evolutionary and statistical properties of three genetic distances. *Molecular Ecology* 11:1263–1273.
- KAREIVA, P. 1990. Population dynamics in spatially complex environments: Theory and data. *Philosophical Transactions of the Royal Society of London, Series B* 330:175–190.
- KERTH, G., F. MAYER, AND E. PETIT. 2002. Extreme sex-biased dispersal in the communally breeding, nonmigratory Bechstein's bat (*Myotis bechsteinii*). *Molecular Ecology* 11:1491–1498.
- KOENIG, W. D., D. VAN VUREN, AND P. N. HOOGE. 1996. Detectability, philopatry, and the distribution of dispersal distances in vertebrates. *Trends in Ecology and Evolution* 11:514–517.
- KOOPMAN, M. E. 2003. Genetic structure of Boreal Owls. Ph.D. dissertation, University of Wyoming, Laramie.
- KOOPMAN, M. E., D. B. McDONALD, G. D. HAYWARD, K. ELDEGARD, G. SONERUD, AND S. G. SERMACH. 2005. Genetic similarity among Eurasian subspecies of Boreal Owls. *Journal of Avian Biology* 36:179–183.
- KOOPMAN, M. E., N. A. SCHABLE, AND T. C. GLENN. 2004. Development and optimization of microsatellite DNA primers for Boreal Owls (*Aegolius funereus*). *Molecular Ecology Notes* 4:376–378.
- KORFANTA, N. M., D. B. McDONALD, AND T. C. GLENN. 2005. Burrowing Owl (*Athene cunicularia*) population genetics: A comparison of North American forms and migratory habits. *Auk* 122:464–478.
- KORPIMÄKI, E., M. LAGERSTRÖM, AND P. SAUROLA. 1987. Field evidence for nomadism in Tengmalm's Owl *Aegolius funereus*. *Ornis Scandinavica* 18:1–4.
- LANDE, R. 1988. Genetics and demography in biological conservation. *Science* 241:1455–1460.
- LEVINS, R. 1969. The effect of random variations of different types on population growth. *Proceedings of the National Academy of Sciences USA* 62:1061–1065.

- LÖFGREN, O., B. HÖRNFELDT, AND B.-G. CARLSSON. 1986. Site tenacity and nomadism in Tengmalm's Owl (*Aegolius funereus* (L.)) in relation to cyclic food production. *Oecologia* 69:321–326.
- LONGMIRE, J. L., A. K. LEWIS, N. C. BROWN, L. M. BUCKINGHAM, L. M. CLARK, M. D. JONES, L. J. MEINCKE, J. MEYNE, R. L. RATLIFF, F. A. RAY, AND OTHERS. 1988. Isolation and molecular characterization of a highly polymorphic centromeric tandem repeat in the family Falconidae. *Genomics* 2:14–24.
- MAJOR, R. E., F. J. CHRISTIE, G. GOWING, AND T. J. IVISON. 1999. Age structure and density of Red-capped Robin populations vary with habitat size and shape. *Journal of Applied Ecology* 36:901–908.
- MANTEL, N. 1967. The detection of disease clustering and a generalized regression approach. *Cancer Research* 27:209–220.
- MARTIN, K., P. B. STACEY, AND C. E. BRAUN. 2000. Recruitment, dispersal, and demographic rescue in spatially-structured White-tailed Ptarmigan populations. *Condor* 102: 503–516.
- MCDONALD, D. B., W. K. POTTS, J. W. FITZPATRICK, AND G. E. WOOLFENDEN. 1999. Contrasting genetic structures in sister species of North American scrub-jays. *Proceedings of the Royal Society of London, Series B* 266:1117–1125.
- MECH, S. G., AND J. G. HALLETT. 2001. Evaluating the effectiveness of corridors: A genetic approach. *Conservation Biology* 15:467–474.
- MILLER, G. S. 1989. Dispersal of juvenile Northern Spotted Owls in western Oregon. M.S. thesis, Oregon State University, Corvallis.
- NEI, M. 1972. Genetic distance between populations. *American Naturalist* 106:283–292.
- NEIGEL, J. E. 2002. Is F_{ST} obsolete? *Conservation Genetics* 3:167–173.
- OYLER-MCCANCE, S. J., N. W. KAHN, K. P. BURNHAM, C. E. BRAUN, AND T. W. QUINN. 1999. A population genetic comparison of large and small-bodied Sage Grouse in Colorado using microsatellite and mitochondrial markers. *Molecular Ecology* 8: 1457–1465.
- PAETKAU, D., W. CALVERT, I. STIRLING, AND C. STROBECK. 1995. Microsatellite analysis of population structure in Canadian polar bears. *Molecular Ecology* 4:347–354.
- PAETKAU, D., L. P. WAITS, P. L. CLARKSON, L. CRAIGHEAD, AND C. STROBECK. 1997. An empirical evaluation of genetic distance statistics using microsatellite data from bear (Ursidae) populations. *Genetics* 147: 1943–1957.
- PRITCHARD, J. K., M. STEPHENS, AND P. DONNELLY. 2000. Inference of population structure using multilocus genotype data. *Genetics* 155:945–959.
- RANNALA, B., AND J. L. MOUNTAIN. 1997. Detecting immigration by using multilocus genotypes. *Proceedings of the National Academy of Sciences USA* 94:9197–9201.
- RAYMOND, M., AND F. ROUSSET. 1995. An exact test for population differentiation. *Evolution* 49: 1280–1283.
- ROSENBERG, D. K., B. R. NOON, AND E. C. MESLOW. 1997. Biological corridors: Form, function, and efficacy. *BioScience* 47:677–687.
- ROUSSET, F. 1997. Genetic differentiation and estimation of gene flow from F -statistics under isolation by distance. *Genetics* 145: 1219–1228.
- RUZZANTE, D. E. 1998. A comparison of several measures of genetic distance and population structure with microsatellite data: Bias and sampling variance. *Canadian Journal of Fisheries and Aquatic Sciences* 55:1–14.
- SAITOU, N., AND M. NEI. 1987. The neighbor-joining method: A new method for reconstructing phylogenetic trees. *Molecular Biology and Evolution* 4:406–425.
- SCRIBNER, K. T., M. R. PETERSEN, R. L. FIELDS, S. L. TALBOT, J. M. PEARCE, AND R. K. CHESSE. 2001. Sex-biased gene flow in spectacled eiders (Anatidae): Inferences from molecular markers with contrasting modes of inheritance. *Evolution* 55:2105–2115.
- SIMBERLOFF, D., J. A. FARR, J. COX, AND D. W. MEHLMAN. 1992. Movement corridors: Conservation bargains or poor investments? *Conservation Biology* 6:493–504.
- SONERUD, G. A., R. SOLHEIM, AND K. PRESTUD. 1988. Dispersal of Tengmalm's Owl *Aegolius funereus* in relation to prey availability and nesting success. *Ornis Scandinavica* 19: 175–181.
- STACEY, P. B., AND M. TAPER. 1992. Environmental variation and the persistence of small populations. *Ecological Applications* 2:18–29.
- SWEANOR, L. L., K. A. LOGAN, AND M. G. HORNOCKER. 2000. Cougar dispersal pat-

- terns, metapopulation dynamics, and conservation. *Conservation Biology* 14:798–808.
- TAKEZAKI, N., AND M. NEI. 1996. Genetic distances and reconstruction of phylogenetic trees from microsatellite DNA. *Genetics* 144:389–399.
- VANDERMEER, J., AND R. CARVAJAL. 2001. Metapopulation dynamics and the quality of the matrix. *American Naturalist* 158: 211–220.
- WALTERS, J. R. 2000. Dispersal behavior: An ornithological frontier. *Condor* 102:479–481.
- WEIR, B. S. 1996. *Genetic Data Analysis II: Methods for Discrete Population Genetic Data*. Sinauer Associates, Sunderland, Massachusetts.
- WEIR, B. S., AND C. C. COCKERHAM. 1984. Estimating *F*-statistics for the analysis of population structure. *Evolution* 38:1358–1370.
- WILCOVE, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. *Ecology* 66:1211–1214.

Associate Editor: K. Winker