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Range-wide genetic differentiation among North American great gray owls (*Strix nebulosa*) reveals a distinct lineage restricted to the Sierra Nevada, California

Joshua M. Hull [a,b,*], John J. Keane [c], Wesley K. Savage [d], Steven A. Godwin [e], Jo Ann Shafer [f], Eric P. Jepsen [c], Rick Gerhardt [g], Chris Stermer [h], Holly B. Ernest [a,i]

[a] *Wildlife and Ecology Unit, Veterinary Genetics Laboratory, 258 CCAH, University of California, One Shields Avenue, Davis, CA 95616, USA*
[b] *Genomic Variation Laboratory, Department of Animal Science, University of California, Davis, CA 95616, USA*
[c] *United States Department of Agriculture, Forest Service, Pacific Southwest Research Station, Sierra Nevada Research Center, 1731 Research Park Drive, Davis, CA 95618, USA*
[d] *Department of Biological Sciences, Lehigh University, Bethlehem, PA 18015-4732, USA*
[e] *Ashland Resource Area, Medford BLM District, 3040 Biddle Road, Medford, OR 97504, USA*
[f] *P.O. Box 3415 Ashland, OR 97520, USA*
[g] *Sage Science, Inc. 319 SE Woodside Ct., Madras, OR 97741, USA*
[h] *California Department of Fish and Game, Wildlife Branch, 1812 Ninth Street, Sacramento, CA 95814, USA*
[i] *Department of Population Health and Reproduction, School of Veterinary Medicine, University of California, One Shields Avenue/Old Davis Road, Davis, CA 95616, USA*

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ABSTRACT

Investigations of regional genetic differentiation are essential for describing phylogeographic patterns and informing management efforts for species of conservation concern. In this context, we investigated genetic diversity and evolutionary relationships among great gray owl (*Strix nebulosa*) populations in western North America, which includes an allopatric range in the southern Sierra Nevada in California. Based on a total dataset consisting of 30 nuclear microsatellite DNA loci and 1938-base pairs of mitochondrial DNA, we found that Pacific Northwest sampling groups were recovered by frequency and Bayesian analyses of microsatellite data and each population sampled, except for western Canada, showed evidence of recent population bottlenecks and low effective sizes. Bayesian and maximum likelihood phylogenetic analyses of sequence data indicated that the allopatric Sierra Nevada population is also a distinct lineage with respect to the larger species range in North America; we suggest a subspecies designation for this lineage should be considered (*Strix nebulosa yosemitensis*). Our study underscores the importance of phylogeographic studies for identifying lineages of conservation concern, as well as the important role of Pleistocene glaciation events in driving genetic differentiation of avian fauna.

1. Introduction

Describing phylogeographic patterns is fundamental to understanding evolutionary processes and informing conservation efforts (e.g., O'Brien, 1994; Avise, 2004; Haig et al., 2004). While phylogeography is primarily a descriptive tool, important conservation insights can be revealed by estimating the relative phylogenetic depth of population divergence, and asking whether geographic populations are genetically distinct lineages, or subpopulations of larger regional genetic groups. Among wide-ranging avian taxa, broad-scale phylogeographic structure is often a result of past climatic and geological events (Avise and Walker, 1998), while fine-scale population differentiation is generally attributed to regional habitat specialization and local adaptation (e.g., Cicero and Johnson, 1998; Cicero, 2004; Hull et al., 2008a). In addition to describing phylogeographic relationships, population-level genetic analyses can aid in ascertaining the recent factors contributing to contemporary patterns of genetic diversity (e.g., estimating rates of recent gene flow) and provide the natural context for informed management approaches that seek to ameliorate further losses of diversity (Funk et al., in press).

The great gray owl (*Strix nebulosa*) is a large-bodied raptor species that ranges throughout Holarctic boreal forests and southward through several montane coniferous forests in Asia and North America (Bull and Duncan, 1993). Two subspecies are currently recognized based on plumage differences and distinct, non-overlapping distributions: *S. nebulosa nebulosa* in North America, and *S. n. lapponica* in Europe and Asia (Bull and Duncan, 1993). The breeding range of great gray owls in North America encompasses the boreal zones of Canada and Alaska, and extends southward into the Rocky Mountains and Cascade Range of the United States. The

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[*] Corresponding author. Address: University of California, Wildlife and Ecology Unit, Veterinary Genetics Laboratory, 258 CCAH, One Shields Avenue, Davis, CA 95616, USA.

E-mail address: jmhull@ucdavis.edu (J.M. Hull).

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Klamath Basin, an important phylogeographic barrier identified in studies of plant and animal taxa (Soltis et al., 1997; Haig et al., 2004), separates the wider range of great gray owls to the north from a disjunct population at the terminus of the species range in the southern Sierra Nevada Mountains in California (Bull and Duncan, 1993). No differences in plumage or morphology have been observed across this barrier; however, the Sierra Nevada population differs from northern populations in migratory behavior, nest site selection, and prey preference (Bull and Duncan, 1993). The great gray owl is a State-endangered raptor in California due to a limited geographic distribution and an estimated statewide census population size of 100–200 individuals (Winter, 1980; Rich, 2000). The core breeding distribution of California great gray owls in the Sierra Nevada is centered in Yosemite National Park and the adjacent Stanislaus and Sierra National Forests. A few individuals have been sporadically documented further north in the Eldorado, Tahoe, and Plumas National Forests and to the south in Sequoia-Kings Canyon National Park and the Sequoia National Forest (Winter, 1986; Rich, 2000; Keane, 2001), but many hundreds of kilometers separate these sightings from the nearest population in southern Oregon.

The Sierra Nevada population of great gray owls may be at high risk of population decline or extinction due to a number of threats. Intense human development pressures at lower elevations threaten both breeding and wintering great gray owl habitat because the foothill regions of the Sierra Nevada are experiencing among the greatest human population growth rates of any region in California (Millar, 1996). Owl habitat at higher elevation is threatened by timber harvest, fire suppression, post-fire salvage harvest, grazing, and alteration of hydrological regimes that has reduced the number of large conifers and oak trees used for nesting, as well as the quality of meadows and forest stands used for foraging (Dull, 1999; Hutto and Gallo, 2006; Saab et al., 2009). West Nile virus infection is also a cause for concern in the Sierra Nevada owl population; while no indication of infection has yet been detected in the wild (Hull et al., 2010), Gancz et al. (2004) reported a 91.3% mortality rate in a captive colony of great gray owls in Ontario, Canada. Additional threats to Sierra Nevada great gray owls include mortality from car strikes, with 30 mortalities documented through 2008 (J. Mauer, Yosemite National Park, pers. comm.; J. Keane unpubl. data), increasing direct and indirect human disturbance resulting from recreational activities, stochastic extinction due to small population size, and increasing summer aridity and air temperatures resulting from climate change (Rauscher et al., 2008; Miller et al., 2009).

Given the small census population size, limited geographic distribution, and number of threats impacting great gray owls in the Sierra Nevada, documenting the phylogenetic relationships among North American populations is necessary to fully assess the conservation status of this isolated population. This information would also provide the context for identifying the level of conservation focus, research, and management action warranted for the Sierra Nevada population, and assist in development of appropriate management strategies. Our objectives for this study were to describe whether great gray owls, given their potential ability for long-range dispersal, are geographically structured across their western North American range. We approached this by generating a combined dataset of molecular markers that we used to address recent and historical population differentiation. With these data, we asked whether the Klamath Basin is a region of reduced gene flow in great gray owls, and explored temporal hypotheses to infer the evolutionary tempo of divergence among great gray owl lineages. We interpreted the results of these analyses in light of the conservation actions that may need to be considered for preserving the Sierra Nevada great gray owl population.

2. Materials and methods

2.1. Population sampling

We collected either whole blood and contour feathers or muscle samples from 93 individual great gray owls (*S. nebulosa*): 8 from western Canada, 25 from southern Oregon, 22 from eastern Idaho, 9 from northern Oregon, and 29 from the southern Sierra Nevada (Fig. 1). Sample collection was limited to adults and nestlings during the breeding season to ensure that samples were accurately associated with a specific geographic range. We only collected samples from individuals presumed to be unrelated. For nestlings, we took samples from a single individual and avoided sampling of adults. Alternatively, when sampling was from adults at nest sites, both parents were included and nestlings were excluded. We drew approximately 0.2 ml of blood from the medial metatarsal vein, and stored it in 1.2 ml of Longmire's solution. We also plucked two contour feathers from each breast. Muscle samples were collected from salvaged fresh great gray owl carcasses. For each of

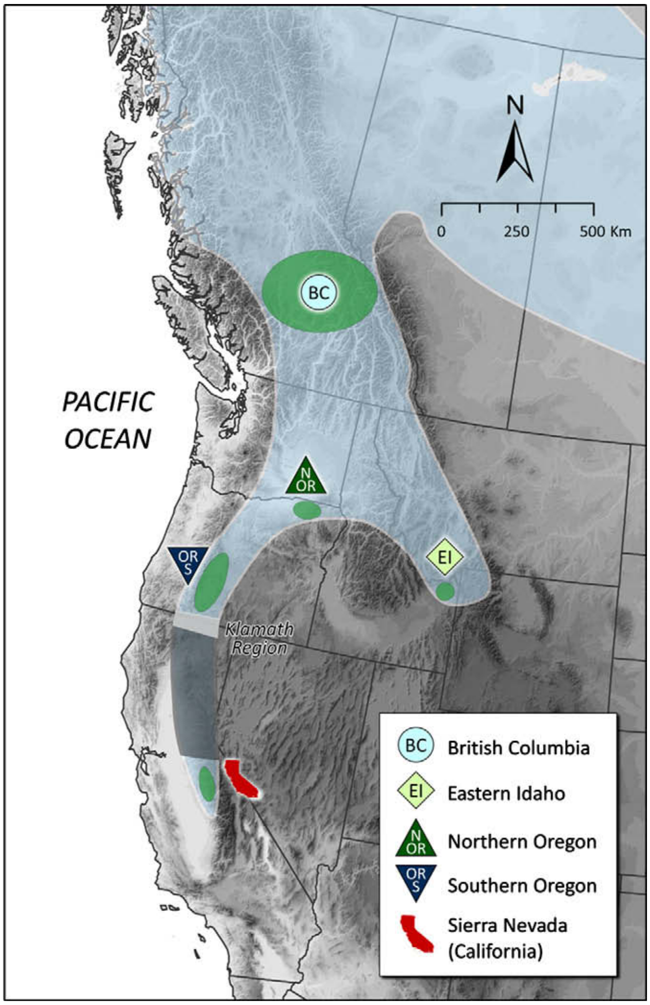

Fig. 1. Western North American range of great gray owls (*Strix nebulosa*; Ridgely et al., 2003). The circular areas illustrate the general sampled regions of population sampling for this study based on the five general regions: the Sierra Nevada, southern Oregon, northern Oregon, eastern Idaho, and western Canada in British Columbia. The Klamath Mountain region, a known phylogeographic barrier, is noted located by the white stippling below the southern Oregon sampling regions. The dark gray stippling identifies a gap in the distribution of great gray owls; this owl species has not been documented between southern Oregon and the southern Sierra Nevada Mountains in California.