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NEWS AND VIEWS

PERSPECTIVE

Restoration of genetic connectivity among Northern Rockies wolf populations

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Probably no conservation genetics issue is currently more controversial than the question of whether grey wolves (*Canis lupus*) in the Northern Rockies have recovered to genetically effective levels. Following the dispersal-based recolonization of Northwestern Montana from Canada, and reintroductions to Yellowstone and Central Idaho, wolves have vastly exceeded population recovery goals of 300 wolves distributed in at least 10 breeding pairs in each of Wyoming, Idaho and Montana. With >1700 wolves currently, efforts to delist wolves from endangered status have become mired in legal battles over the distinct population segment (DPS) clause of the Endangered Species Act (ESA), and whether subpopulations within the DPS were genetically isolated. An earlier study by vonHoldt *et al.* (2008) suggested Yellowstone National Park wolves were indeed isolated and was used against delisting in 2008. Since then, wolves were temporarily delisted, and a first controversial hunting season occurred in fall of 2009. Yet, concerns over the genetic recovery of wolves in the Northern Rockies remain, and upcoming District court rulings in the summer of 2010 will probably include consideration of gene flow between subpopulations. In this issue of *Molecular Ecology*, vonHoldt *et al.* (2010) conduct the largest analysis of gene flow and population structure of the Northern Rockies wolves to date. Using an impressive sampling design and novel analytic methods, vonHoldt *et al.* (2010) show substantial levels of gene flow between three identified subpopulations of wolves within the Northern Rockies, clarifying previous analyses and convincingly showing genetic recovery.

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With samples from all 66 re-introduced founders to Yellowstone and Central Idaho, as well as 555 samples over the first 10 years of recovery (1995–2004), the analysis by vonHoldt *et al.* (2010) of Northern U.S. Rockies wolf population structure and gene flow is one of the most intensive efforts ever conducted for an endangered species. Classic landscape genetic methods were difficult to apply because of the recent and complex founder history of the populations. To deal with these challenges, vonHoldt *et al.* (2010) developed pioneering methods combining assignment tests, private alleles and an especially compelling reconstruction of sibship patterns to identify genetically effective dispersers. These methods were uniquely coupled with an interdisciplinary approach to better define population clusters based on Bayesian analyses of genetic data (an approach with known limitations; Schwartz & McKelvey 2008) combined with ecological information on wolf movements. For example, a unique strength of vonHoldt *et al.*'s (2010) methods was the validation of genetically identified 'migrants' with extensive field data on radiocollared dispersers. The methods they developed will be of direct utility in other endangered species for which precise estimates of gene flow are essential.

Fig. 1 Gene flow in action between the alpha wolf pair from the Mt. Everts wolf pack in Yellowstone National Park, 2008. This photograph illustrates the critical importance of assessing gene flow with genetic methods in combination with field ecology. Photograph credit: Dan Stahler/National Parks Service.

Their methodology unequivocally establishes that conservation genetic metrics of recovery mirror the wildly successful demographic increase of Northern Rockies wolves. With an average annual increase of 27% per year over the 10-year study, the total population grew from 101 to 846. vonHoldt *et al.* (2010) demonstrate – as theory would predict – that this demographic success has been matched genetically, with high levels of retained genetic diversity and low levels of inbreeding (indeed, even strong inbreeding avoidance; see also vonHoldt *et al.* 2008). Furthermore, and critical to the legal deliberations, genetically effective dispersal between the three main subpopulations in northwestern Montana, Idaho and Wyoming was documented and quantified. Their minimum estimate of 3–5 migrants per generation was, the authors note, almost certainly low by at least half because only about 30% of the wolves were sampled. As the wolf population has doubled in size and expanded in space since the study ended in 2004, even more migrants are expected at the present time. High levels of gene flow are consistent also with independently collected radiotelemetry data (Smith *et al.*2010). Thus, both genetic data and telemetry imply gene flow above rules of thumb for minimizing heterozygosity loss in subpopulations, such as the one (to ten) migrants per generation rule (Mills & Allendorf 1996).

vonHoldt *et al.* (2010) also confirm the genetic legacy of the founding wolves in the 3 subpopulations in Idaho, Yellowstone and northwestern Montana. Despite high levels of genetic diversity and gene flow, the authors found a strong signal of subpopulation division within the Northern Rockies. This provides support for the current metapopulation approach that treats each subpopulation as a management unit (USFWS 2009). However, founder effects may attenuate in the future because of the levels of gene flow observed in this study (e.g. Fig. 1), especially compared to other re-introduced species with lower dispersal ability than wolves (Biebach & Keller 2009; Williams & Scribner 2010). The study by vonHoldt *et al.* (2010) also implies gene flow between the subpopulation of Yellowstone National Park (YNP) and the surrounding Greater Yellowstone Ecosystem (GYA) and adjacent subpopulations in Idaho and in NW Montana. In an earlier, more limited effort focused just on YNP, however, vonHoldt *et al.* (2008) found no dispersal into the YNP wolf population. Based on this, they concluded YNP was genetically isolated and even at risk of extirpation because of the potential for inbreeding depression (vonHoldt *et al.* 2008).

Given the different conclusions of these two papers, some perspective is required. In the first study, where vonHoldt *et al.* (2008) documented no gene flow into the high-density YNP, the analysis did not examine the surrounding GYA, with lower wolf density. Perhaps, by focusing just on YNP, which was likely at carrying capacity (and thus difficult for a dispersing wolf to successfully immigrate into), vonHoldt *et al.* (2008) did not examine gene flow at the appropriate subpopulation level. On the other hand, in this most recent study, the GYA may be an important region with some vacant habitat available for wolf dispersal and therefore bridging gene flow with YNP.

In vonHoldt *et al.* (2008), the VORTEX simulation of the effects of inbreeding depression on wolf viability was also flawed by some key assumptions about wolf ecology and behaviour, including underestimating gene flow to the GYA subpopulation, exaggerating estimates of the deleterious effects of inbreeding on demography and overestimating the levels of gene flow required to avoid inbreeding depression. For example, the number of immigrants required to prevent 'significant decreases' in heterozygosity and increases in inbreeding was based on an arbitrary threshold of 1% over 100 years; because 100 years represents about 25 wolf generations, this threshold is 25 times higher than, for instance, the 1% *per generation* threshold used to derive the effective population size of '50' in the famous '50–500' rule (Soulé 1980). Overall, the analyses from this most recent study (vonHoldt *et al.* 2010), in concert with other findings of genetic rescue in wolves (Vila *et al.* 2003; Hedrick & Fredrickson 2010), obviate the concerns raised by the earlier vonHoldt *et al.* study about isolation of YNP wolves.

Finally, the study provides clear lack of evidence for the genetic legacy of any remnant 'native' wolf population. All genotyped wolves could be successfully assigned to either Montanan (naturally recolonized) or re-introduced wolves. This should effectively lay to rest a growing public concern amongst the anti-wolf public that re-introduction is illegal because it re-introduced a non-native subspecies, the 'Canadian' wolf (*Canis lupus occidentalis*, Richardson 1829) into extant native populations of 'Northern Rocky Mountain' wolves (*Canis lupus irremotus* [sic], *Canis lupus nubilus*, Say 1823)(Nowak *et al.* 2003) (Urbigkit 2008). Although far-fetched, especially given the near-impossibility of a native wolf population remaining undetected (Patterson 2010), potential litigation concerning 'remnant' wolves underscores the importance of vonHoldt *et al.*'s (2010) findings.

In conclusion, concerns that this highly vagile and fecund species might suffer negative effects of genetic isolation between the 3 established wolf subpopulations have been effectively laid to rest by vonHoldt *et al.*'s (2010) exhaustive work. Such connectivity may or may not be maintained in years to come, as more liberal management is expected for wolves living outside protected core areas. The pioneering work by vonHoldt *et al.* (2010) has established the ecological and evolutionary baseline for future monitoring of the effects of wolf management in the Northern Rockies, as governance moves away from managing wolves as endangered. This work also illustrates a new standard for methodological approaches in molecular ecology for the conservation of re-introduced species. Such molecular ecology analyses that combine demography (including radiotelemetry) and population genetics at the meta-population-level and at a larger scale (Western US and Canada) are the next logical step in ensuring successful management post-delisting.

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