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NEWS AND COMMENTARY

Genetics of wolf conservation

Genetics and wolf conservation in the American West: lessons and challenges

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Top predators are endangered throughout the world because of human persecution and habitat destruction. Plans to conserve and restore predator populations are often contentious, but few species are as problematic as the gray wolf (*Canis lupus*). In the United States, wolf conservation policy and management has often been schizophrenic, ranging from predator control and open hunting to reintroduction and absolute protection. Likewise, public and scientific opinion is equally divided between those who maintain that wolves are an essential part of ecosystems and provide top-down effects contrasting with those who believe wolves cannot readily coexist with humans, especially in landscapes dominated by ranching or farming. In the American West, there have been large-scale reintroductions of the gray wolf (*C. lupus nubilus*) in the Northern Rocky Mountains (NRMs) and the Mexican wolf (*C. lupus baileyi*) in the southwest, which provide important lessons for reintroduction efforts elsewhere. In this study, we specifically discuss wolf conservation in the American West in relation to critical genetic factors that affect restoration, recovery and conservation. We also discuss the natural colonization of wolves in Sweden and Norway, and discuss a synthesis of problems and solutions in the large-scale recovery of wolves.

Wolves in the Northern Rocky Mountains

The gray wolf is an enduring symbol of the wild and once ranged throughout the Rocky Mountains and coastal ranges of Western North American. Genetic analysis suggests several hundred thousand wolves existed in these habitats and wolves now living in Canada and Alaska represent just a subset of the historical variation that once existed in the American West (Leonard *et al*., 2005). Wolves were essentially exterminated from the NRMs by the mid 20th century and reintroduction to Yellowstone National Park and central Idaho (see Figure 1) was initiated in 1995 with wolves from the Canadian Provinces of British Columbia and Alberta. The fact that wolves from these areas represent a subset of genetic variation found in the American West means that the reintroduced wolves are not alien species as some have asserted, rather these wolves re-established a historical legacy that derives from the Old World migration of the gray wolf to North America several hundred thousand years ago.

The NRM reintroductions used wild-caught individuals and translocated them in large numbers: 31 individuals to Yellowstone and 35 to central Idaho in 1995 and 1996. These two areas, along with a Montana population that was naturally re-established starting in 1979, define the three areas in the recovery plan for the Western wolf under the US Endangered Species Act. Recovery was to be considered successful if simultaneously each area had at least 100 individuals in 10 packs for a period of 3 years, and these populations were connected by genetically effective migration. There are now about 1600 wolves in the three areas, and they have been delisted (removed from federal protection under the Endangered Species Act) and are under state management in two of the three recovery areas. Recent research has suggested that wolves have initiated a trophic cascade in Yellowstone National Park, allowing for the restoration of forest and other native vegetation in overgrazed grassland (Ripple *et al*., 2001; Fortin *et al*., 2005). Nonetheless, scientific, political and moral issues continue to hamper wolf recovery for what is, otherwise, the most successful restoration of a large carnivore to its native habitat.

Several basic scientific problems need to be addressed before recovery is considered successful. First, is the total of 300 individuals in 30 packs enough for long-term sustainability? Stochastic population models of large carnivores show that isolated populations of less than 100 individuals often have a high chance of extinction. Further, genetic loss could be consequential because wolf packs generally have only a single breeding (alpha) pair. The effective population size (N_e) determines how rapidly genetic variation is lost and is closely related to the number of breeders, and how equitably they breed. Consequently, the N_e may be only 20 or less for the 10 packs in each population. If isolated, these populations would lose $1/(2N_e)$ of genetic heterozygosity, or about 2.5%, per generation. Fortunately, the number of wolves has expanded well beyond these minimum numbers, and the loss of genetic variability has been negligible (vonHoldt *et al*., 2008, 2010). The question is then, what will happen if western states allow the population to be hunted to the federal minimum requirement for recovery (the enacted State plans actually required a higher figure of 15 packs or 150 individuals)? Such small populations would also be more vulnerable to random demographical and genetic affects and could sink far below the minimum numbers. Unfortunately, the 10 by 10 designation for each of the three recovery areas was not based on quantitative and model-based science, but instead reflected primarily a survey of 'expert' opinion.

Second, for long-term persistence, these three sub-populations need to be connected by genetically effective migration. In a recent detailed genetic study, vonHoldt *et al*. (2010) estimated that the genetically effective migration rate between the Idaho and Montana sub populations was adequate at >3 migrants per generation. However, the Yellowstone National Park population seemed to be isolated and received no natural migrants that reproduced over a 10-year period. This may reflect the difficulty that migrant wolves have in reproducing in a saturated wolf system such as Yellowstone. This study found that migrants are successful outside the Park in the Greater Yellowstone Ecosystem where there is more turnover, but these migrants and their ancestry may not help augment the genetic diversity in the Park. Further, hunting is now allowed under State management plans to the border of the Park, and recently two radiocollared wolves were killed, one of which was a breeder. The Park population has further been reduced by 40% from

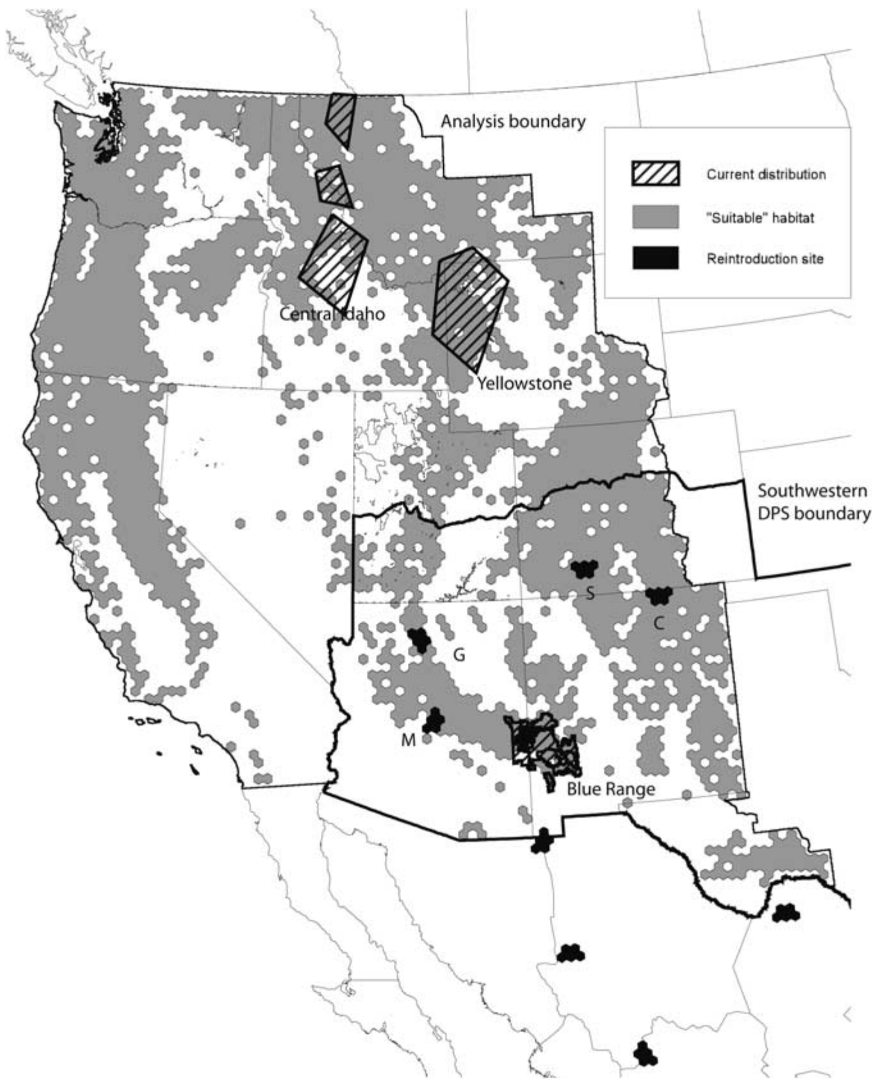

Figure 1 Areas currently occupied by Northern Rocky Mountain wolves (courtesy of C. Carroll). The three recovery areas are Northern Montana (the northmost hatched area), Central Idaho and the Greater Yellowstone Area. The reintroduction site of the Mexican wolf in the Blue Range Recovery area and the locations of four additional recovery areas on the north rim of the Grand Canyon (G), central Arizona (M) and Northern New Mexico-Southern Colorado (S and C) (Carroll *et al*., 2006).

disease and most recently, the Druid Pack, the most notable and reproductively successful pack in the history of the re-introduction has disbanded. Whether population declines because of hunting and predator management as well as natural factors such disease and changes in prey base, may actually improve opportunities for genetically effective migration into the Park or accelerate the loss of genetic variation and heighten the probability of local extinction is not certain. However, such concerns highlight the continued need for population management and monitoring.

Third, the three-recovery area plan needs a realistic future. Given that several hundred wolves are orders of magnitude fewer than the West supported in the past, or could support now even given the loss of habitat, what plans should be made for the long term? In Yellowstone, wolves have substantially reduced coyote numbers in many areas and may also have had top-down positive effects on the abundance of certain prey, such as pronghorn antelope (Berger *et al*., 2008). Wolves in the West are expanding their range and have been documented in Colorado, Oregon, Utah and Washington State. A management plan is possible that transcends state boundaries and aims to re-establish genetically interconnected wolf populations that can persist into the future and focuses on areas where they provide ecosystem, societal and economic benefit with minimum human conflict.

The Mexican wolf

The history of the Mexican wolf, the smallest and most highly endangered of the North American wolves, is surrounded by controversy and mystery. The Mexican wolf, an endangered subspecies of the gray wolf, is the most genetically distinct wolf subspecies in North America (Leonard *et al*., 2005). Landscape changes and government and private bounty hunting throughout its range reduced and isolated Mexican wolf populations so that by 1925 they were rare in the United States and extinct by the 1970s. As a result, the Mexican wolf subspecies was listed as endangered in 1976. Only a few Mexican wolves remained in isolated groups in Mexico by 1980 and surveys since have not detected any wild Mexican wolves there or elsewhere.

All Mexican wolves alive today descend from three captive lineages founded between 1960 and 1980 from a total of seven wolves (Hedrick *et al*., 1997). In 1998, a population of 13 Mexican wolves was introduced to Eastern Arizona and Western New Mexico (known as the Blue Range population or BRP) and 65 wolves in total were introduced from 1998 to 2001 (Figure 1). Initially these wolves had only ancestry from one of the lineages with only three founders, but starting in 2000 wolves with ancestry from more than one lineage have been released (Hedrick and Fredrickson, 2008). As of January, 2010, there were only 42 wolves that could be detected in this reintroduced population (a very small number compared with the two introduced NRM populations, which had minimum numbers of 739 and 390 for the Yellowstone and Idaho populations at an equivalent time after translocation), a number that has declined from 59 in 2006. Further, there were only two breeding pairs in the population at the end of 2009 (defined as a pair with at least two young-of-year pups present at the end of the calendar year).

The initial reintroduction in 1998 was followed by further releases in subsequent years, but no documented successful reproduction and recruitment in the wild until 2003. Part of the initially slow success seems to have been because the reintroduced individuals were drawn from a naïve captive population, but after reproduction started it seemed that the population would continue to grow and become self sustaining. However, from 2005 to 2007, 62 animals were removed, many from the most successful packs, primarily because of depredation claims. These large-scale removals and the near cessation of reintroduction actions fundamentally altered the trajectory of the population. In addition, Fredrickson *et al*. (2007) showed that part of the slow increase in population size was attributable to the low fitness in the population. Evaluation of litter size and other fitness components showed that crosses between the lineages had increased fitness both in captivity and in the reintroduced population (Fredrickson *et al*., 2007), but management actions did not capitalize on this benefit from genetic rescue (Hedrick and Fredrickson, 2010). Further, since 1998, at least 32 animals have been illegally killed and in only two cases has the killer been identified and successfully prosecuted (four more alpha males have been killed or have gone 'missing' in the late spring-early summer of 2010). Overall, human-caused mortality from illegal killing and road kills, and removals mainly due to human conflict, have severely impacted the ability of this population to increase.

Although genetic considerations are important in the recovery of the reintroduced Mexican wolf, some management policies and actions have had quite detrimental effects on the reintroduced population. First, the reintroduced population is limited in range and individuals that leave the recovery area are generally caught or killed. Second, initial releases of captive wolves with no previous wild experience is limited to a small area in Arizona and not permitted in New Mexico, which contains some of the best wolf habitat. The cumulative effects of wolf removals primarily because of boundary issues and livestock depredations, caused the overall removal/mortality rate (64%) to exceed that predicted (47%) for the reintroduced population in the first 5 years. For the BRP to compensate for the high mortality, the recruitment rate needs to be quite high. Because there have been few new introductions recently, in combination with the low fitness of some of the alpha wolves from a single lineage, persistence of the reintroduced population is in question.

Although the problems faced with the single reintroduced population are great, for long-term recovery, the success of this population is only a start. In our opinion, the recovery objectives of the NRM wolves can only be used as a starting point for recovery of Mexican wolves. There is no recent recovery plan for Mexican wolves and two more recovery team efforts in the mid 1990s and 2000s to write recovery plans were aborted. For example, having three populations connected by significant gene flow seems to be a reasonable recovery objective for Mexican wolves. However, Mexican wolves are quite different from NRM wolves because they all descend from captive animals, have initially a much higher level of inbreeding, suffer a higher rate of human-caused mortality, and from the recent experience with the Blue Range population, have a much more precarious probability of persistence. Given expected rates of wolf removal and killing, we suggest that for recovery of Mexican wolves three populations, each simultaneously having 250 animals for 8 years (approximately two generations) is the minimum necessity. These recovery goals need to be supported with rigorous demographical models and investigation. Because new wolves come from captivity and there is a small founder number from three different lineages, extensive management is necessary for successful recovery. The negative impacts on the population from the moratorium that was placed on reintroductions and the large-scale removals during the period from 2005 to 2009 shows a critical need for scientifically based management.

Using a sophisticated landscape analysis, potential sites for the additional populations have been identified (Carroll *et al*., 2006) (Figure 1). In particular, the north rim of the Grand Canyon (indicated as G) and Northern New Mexico Southern Colorado sites (S and C) seem most appropriate for these two additional populations. The experience of introducing wolves to the Blue Range identifies the need to control human-caused mortality and initially intensive management in these populations. In addition, if natural gene flow does not occur between these populations, then artificial movement between the populations may be necessary.

The Scandinavian recolonization

Perhaps, the gray wolf situation with the most parallels to the NRM and Mexican wolf cases is the contemporary Scandinavian wolf population in Sweden and Norway that seems to have been established by a pair of animals that naturally immigrated in the early 1980s. The number remained at less than ten individuals in a single pack during the 1980s. A third male founder naturally migrated from the Finland–Russia population around 1990, resulted in genetic (or behavioral) rescue, and the population increased to around 100 individuals (Vilá *et al*., 2003). Subsequently, the amount of inbreeding greatly increased and there was a significant decline in the number of surviving pups per litter (Liberg *et al*., 2005). Two additional male migrants started breeding in 2008 and have produced three litters apiece with a total of about 40 pups (Olof Liberg, personal communication). The estimated total number in early 2010 is 200–240 with about 26–32 in Norway. The Norwegian government has killed a number of wolves in the small part of the population residing in Norway in 2001 (9 out of 28 killed) and 2005 (5 out of 18–21). The Swedish government has now authorized hunting to maintain a limit of 210 wolves in Sweden. The Swedish population has been closely monitored at substantial expense, and remains the clearest example of the importance of genetically successful migration for recovery. However, management actions act to counteract such benefits. The contrast with the American West where genetically effective migration is a requirement for delisting, argues for the importance of strong scientifically based legislation for endangered species recovery elsewhere.

Lessons and challenges

The reintroduction of gray wolves to the NRM and Mexican wolves to the BRP provide extreme outcomes for wolf reintroduction. The NRM wolves, which derive from wild populations, grew rapidly and have generally met the recovery goals in little more than a decade. In contrast, the lone Mexican wolf population, originally derived from a single inbred population, is not increasing and its long-term survival is in question. In both cases, scientific priorities have at times been ignored given political considerations. From the NRM reintroduction, it is clear that wolves are resilient and have the potential for population growth, dispersal and adaptability. The challenge will be to harness these characteristics in a scientifically justified plan that we have the will and political acumen to implement. Genetic rescue is a reality in large carnivores and genetically effective migration is a critical variable in population management, given that large carnivores demand so much pristine habitat that is rapidly becoming subdivided by roads and human development.

Conflict of interest

The authors declare no conflict of interest.

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Berger KM, Gese EM, Berger J (2008). Indirect effects and traditional trophic cascades: a test involving wolves, coyotes, and pronghorn. *Ecology* **89**: 818–828.
Carroll C, Phillips MK, Lopez-Gonzalez CA, Schumaker NH (2006). Defining recovery goals and strategies for endangered species: the wolf as a case study. *BioScience* **56**: 25–37.
Fortin D, Beyer HL, Boyce MS, Smith DW, Duchesne T, Mao JS (2005). Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology* **86**: 1320–1330.
Fredrickson RJ, Siminski P, Woolf M, Hedrick PW (2007). Genetic rescue and inbreeding depression in Mexican wolves. *Proc R Soc B* **274**: 2365–2371.
Hedrick PW, Fredrickson RJ (2008). Captive breeding and the reintroduction of Mexican and red wolves. *Molec Ecol* **17**: 344–350.
Hedrick PW, Fredrickson RJ (2010). Genetic rescue: guidelines an example from Mexican wolves and Florida panthers. *Cons Genet* **11**: 615–626.
Hedrick PW, Miller PS, Geffen E, Wayne RK (1997). Genetic evaluation of the three captive Mexican wolf lineages. *Zoo Biol* **16**: 47–69.
Leonard JA, Vila C, Wayne RK (2005). Legacy lost: genetic variability and population size of extirpated US grey wolves (*Canis lupus*). *Mol Ecol* **14**: 9–17.
Liberg O, Andrén H, Pederson H-C, Sand H, Sejbeg D, Wabakken P *et al*. (2005). Severe inbreeding depression in a wild wolf (*Canis lupus*) population. *Biol Lett* **1**: 17–20.
Ripple WJ, Larsen EJ, Renkin RA, Smith DW (2001). Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. *Biol Cons* **102**: 227–234.
Vilá C, Sundqvist A-K, Flagstad Ø, Seddon J, Björnerfeldt S, Kojola I *et al*. (2003). Rescue of a severely bottlenecked wolf (*Canis lupus*) population by a single immigrant. *Proc R Soc B* **270**: 91–97.
vonHoldt BM, Stahler DR, Smith DW, Earl DA, Pollinger JP, Wayne RK (2008). The genealogy and genetic viability of reintroduced Yellowstone grey wolves. *Mol Ecol* **17**: 252–274.
vonHoldt BM, Stahler DR, Bangs EE, Smith DW, Jimenez MD, Mack CM *et al*. (2010). A novel assessment of population structure and gene flow in grey wolf populations of the Northern Rocky Mountains of the United States. *Mol Ecol* **19**: 4412–4427.

Editor's suggested reading

Rutledge LY, Garroway CJ, Loveless KM, Patterson BR (2010). Genetic differentiation of eastern wolves in Algonquin Park despite bridging gene flow between coyotes and grey wolves. *Heredity* **105**: 520–531.
Alcaide M, Serrano D, Negro JJ, Tella JL, Laaksonen T, M üller C *et al*. (2009). Population fragmentation leads to isolation by distance but not genetic impoverishment in the philopatric Lesser Kestrel: a comparison with the widespread and sympatric Eurasian Kestrel. *Heredity* **10**: 190–198.
Lachish S, Miller KJ, Storfer A, Goldizen AW, Jones ME (2011). Evidence that disease-induced population decline changes genetic structure and alters dispersal patterns in the Tasmanian devil. *Heredity* **106**: 172–182.