



Reevaluating and Broadening the Definition of Genetic Rescue

A widely accepted definition of *genetic rescue* from the classic review by Tallmon et al. (2004) is: “when population fitness, inferred from some demographic vital rate or phenotypic trait, increases by more than can be attributed to the demographic contribution of immigrants.” However, this definition limits assessment of the success of genetic rescue, decreases the probability of detecting benefits of genetic rescue, and thus restricts application of genetic rescue in increasing the viability of endangered species and populations. More specifically, there is reason to expect the demographic benefits of genetic rescue may be masked if environmental conditions are limiting or deteriorating, a situation that may have been previously overlooked because instances of genetic rescue receiving the most attention involve environmental conditions that permitted population expansion (Bouzat et al. 2009; Hedrick & Fredrickson 2010). As a result, one needs to consider more carefully the definition of, and standards for, assessing genetic rescue and include documentation of genetic change in ancestry following genetic rescue.

The loss of genetic viability is a critical and widespread threat to threatened and endangered species and populations. Genetic rescue, which entails the introduction of unrelated individuals, is a potentially important tool to increase the viability of such populations (Tallmon et al. 2004). Despite its potential, <10 cases of genetic rescue have been well documented (Adams et al. 2011). Obstacles to the collection of adequate data to assess genetic rescue are widely appreciated; however, there is likely an additional, unappreciated obstacle to assessing genetic rescue. That impediment is the very definition of *genetic rescue* and the standards used to judge whether genetic rescue has occurred. The need to reconsider the definition of genetic rescue is revealed when one compares how several well-studied populations have responded to the introduction of unrelated individuals.

First, when Texas pumas were artificially introduced into the endangered Florida panther population (both

are *Puma concolor*), the population expanded into new areas as it increased from around 25 to over 100 individuals in just over a decade (Johnson et al. 2010). Similarly, the Swedish wolf population (*Canis lupus*) naturally reestablished itself in the early 1980s with 2 migrants from Finland. The population consisted of a single pack until another male wolf immigrated into the population around 1990 (Vilà et al. 2003). As a result of this natural genetic-rescue event, the population quickly increased to over 200 individuals by populating previously unoccupied areas. In contrast, the immigration of an individual into the wolf (*Canis lupus*) population on Isle Royale (U.S.A.), an island in Lake Superior (Adams et al. 2011), was not followed by an increase in abundance, a demographic measure of population fitness. Prior to the immigration event, every portion of Isle Royale had been occupied by a wolf pack for approximately 50 years; thus, there was no opportunity for the population to increase by expanding into available habitat.

Second, deteriorating environmental conditions may be common to many populations of conservation concern and may obscure the demographic benefits of genetic rescue. For example, the immigration of the male wolf to Isle Royale coincided with a substantial decline in moose (*Alces alces*), their main prey. In contrast, prey was plentiful after the genetic-rescue events for Florida panthers and Swedish wolves.

Third, for both Florida panthers and Swedish wolves genetic changes associated with genetic rescue were confirmed by detailed pedigree analysis with molecular genetic markers. The ancestral contribution of the 5 successfully contributing Texas pumas in the total Florida panther population was approximately 41% (Johnson et al. 2010), and the contribution from the Swedish wolf immigrant was around 30% (Liberg et al. 2005). The 1997 immigration of the male wolf to Isle Royale was only discovered in 2009 in an examination of molecular data. Subsequent pedigree analysis revealed the fitness of this immigrant so exceeded that of native wolves that

within 10 years he was related to every individual in the population and his ancestral contribution was 56% of the population (Adams et al. 2011). This astonishing genomic sweep is strong evidence that fitness was low among native Isle Royale wolves relative to the fitness of the immigrant wolf and his descendants. In other words, the effect of genetic rescue in the Isle Royale case appears even greater than the effect in the Swedish wolf and Florida panther populations, which had classical ecological responses to genetic rescue. These examples show that effort and money used to monitor and understand genetic changes is well directed.

The Isle Royale wolves reveal another underappreciated challenge to assessing genetic rescue. If one could compare the fitness observed after the arrival of the immigrant in relation to what fitness would have been (in the face of deteriorating environmental conditions) had the immigrant not arrived, then it seems very likely that genetic rescue benefited fitness and demography. Because such a comparison is conceptually impossible, it may be valuable to reconsider the definition of genetic rescue for cases like this. A useful definition of *fitness* in this context is that it “refers to the capacity of a variant type to invade and displace the resident population in competition for available resources” (Demetrius & Ziehe 2007). Using this characterization of fitness, the definition of *genetic rescue* of Tallmon et al. (2004) should be expanded to be (1) “when population fitness, inferred from some demographic vital rate or phenotypic trait, increases by more than can be attributed to the demographic contribution of immigrants” or (2) when the environmental conditions are thought to be limiting or deteriorating and genetic analysis of ancestry demonstrates a contribution of recent immigration significantly greater than expected by chance from genetic drift. This addition to the definition of *genetic rescue* makes genetic analyses of the change in ancestry fundamental.

Acknowledgments

P.W.H. acknowledges the support of the Ullman Distinguished Professorship and J.R.A. and J.A.V. acknowledge the support of the National Science Foundation (DEB-06137730 and DEB-0424562).

Philip W. Hedrick,* Jennifer R. Adams,†‡ and John A. Vucetich†

*School of Life Sciences, Arizona State University, Tempe, AZ 85287-4501, U.S.A., email philip.hedrick@asu.edu

†School of Forest Resources and Environmental Science, Michigan Technological University, Houghton, MI 49931, U.S.A.

‡Current address: Department of Fish and Wildlife Resources, University of Idaho, Moscow, ID 83844, U.S.A.

Literature Cited

- Adams, J. R., L. M. Vucetich, P. W. Hedrick, R. O. Peterson, and J. A. Vucetich. 2011. Genomic sweep and potential genetic rescue during limiting environmental conditions in an isolated wolf population. *Proceedings Royal Society London B* DOI:10.1098/rspb.2011.0261.
- Bouzat, J. L., J. A. Johnson, J. E. Toepfer, S. A. Simpson, T. L. Esker, and R. L. Westemeier. 2009. Beyond the beneficial effects of translocations as an effective tool for the genetic restoration of isolated populations. *Conservation Genetics* **10**:191–201.
- Demetrius, L., and M. Ziehe. 2007. Darwinian fitness. *Theoretical Population Biology* **72**:323–345.
- Hedrick, P. W., and R. Fredrickson. 2010. Guidelines for genetic rescue: examples from Mexican wolves and Florida panthers. *Conservation Genetics* **11**:615–626.
- Johnson W. E., et al. 2010. Genetic restoration of the Florida panther. *Science* **329**:1641–1645.
- Liberg, O., H. Andrén, H. C. Pedersen, H. Sand, D. Sejberg, P. Wabakken, M. Åkesson, and S. Bensch. 2005. Severe inbreeding depression in a wild wolf (*Canis lupus*) population. *Biology Letters* **1**:17–20.
- Tallmon, D. A., G. Luikart, and R. S. Waples. 2004. The alluring simplicity and complex reality of genetic rescue. *Trends in Ecology & Evolution* **19**:489–496.
- Vilà, C., A. K. Sundqvist, Ø. Flagstad, J. Seddon, S. Björnerfeldt, I. Kojola, A. Casulli, H. Sand, P. Wabakken, and H. Ellegren. 2003. Rescue of a severely bottlenecked wolf (*Canis lupus*) population by a single immigrant. *Proceedings Royal Society London B* **270**:91–97.

