Population Biology and Herpetological Conservation: A Cautionary Note

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Abstract

Common endangered species conservation management practices, such as translocations and captive breeding and release of individuals, tend to mix populations. This mixture is most often assumed to be beneficial because it increases effective population size and may also increase genetic variation. However, when populations are adapted to different local conditions, mixing populations can dilute local adaptation and could theoretically result in population declines. Resource managers should therefore be careful when the mixture of populations is considered, particularly in low dispersing species that are prone to local adaptation, such as salamanders.

Key Words

Demographics, gene flow, conservation, populations, management, inbreeding depression, amphibian, reptile

Major concerns for small population management

There are two major concerns in the conservation of small populations: genetic and demographic factors. The genetic factors are inbreeding depression and the loss of genetic variation through genetic drift. Inbreeding depression threatens and reducing small populations with the possibility of unmasking recessive deleterious alleles and a reduction in

heterozygosity. Each of these factors can, in turn, affect individual fecundity and consequently reduce population growth. When genetic variation is lost, a population may decline because of its potential inability to track environmental shifts (Frankel and Soulé 1981; Lande and Barrowclough 1987). Demographic factors, such as the allee affect, where a population is so small that individuals have difficulty finding mates, can also severely affect small popu-



lations. These factors are becoming more widely recognized as tantamount to species extinction's (Lande 1988; Schemske, et al. 1994).

There is some debate about whether genetic or demographic factors should be the primary focus in the study and management of small populations. However, the conservation programs that deal specifically with threatened or endangered populations are often solutions to both problems. These management schemes include: movement corridors between nature reserves, captive breeding and release of individuals, and translocations of individuals between populations. All of these strategies tend to enhance gene flow, or the movement of individuals and the integration of their genes, among populations.

The issue of Gene Flow

All of these potential solutions, therefore, are based upon the assumption that gene flow is beneficial to managed populations. Population genetic theory indicates that gene flow can act as a "creative force" by maintaining genetic variation and increasing effective population size and thus combating the negative consequences of inbreeding depression and demographic stochasticity (Slatkin 1987). However, there has been little consideration of the potential detrimental effects that gene flow may have on populations despite the theory and empirical data to support such effects. For example, high levels of gene flow among populations with different environments (and consequently different selection regimes) can swamp local adaptation and drive populations to adapt to the average of local conditions (Wright 1951; Slatkin 1987); therefore, populations are not well adapted. Associated with this swamping of local adaptation can be a reduction in fitness, which is known as outbreeding depression (Templeton 1986). In the long-term, gene flow can also preclude subpopulation differentiation and eventually prevent speciation by maintaining genetic contact (Mayr 1963, 1969).

Along with many examples of the enhancement of gene flow resulting in the decline of managed populations (see Greig 1979), there are also examples of gene flow acting as an evolutionary constraint for natural amphibian and reptile species. A well-known reptilian example is the Lake Erie water snake, Nerodia sipedon. Banded snakes were found to be more cryptic (and much more common) in the wooded areas of the mainland surrounding Lake Erie, and

unbanded snakes were more common and cryptic in the open, rocky areas of the islands (Camin and Ehrlich 1958; King 1992). Varying degrees of banding have consistently been found in the juvenile island populations, despite its selective disadvantage (Camin and Ehrlich 1958; King 1987). Observations of snake dispersal and recent estimates of gene flow indicated that individuals were dispersing from the mainland to the islands (King 1987). Quantitative genetic analyses indicated that color pattern was largely genetically determined and that selection, in the absence of gene flow, was strong enough to eliminate the noncryptic (or banded) morph on the islands (King 1993a). King recently concluded that gene flow from the mainland population was overwhelming the effect of selection, which caused an observed decline in population fitness (King 1987, 1993*a*, 1993*b*).

One amphibian example comes from research on the stream-breeding salamander, Ambystoma barbouri. In some streams that are deep enough to support permanent pools, A. barbouri larvae face a major selection pressure that comes from predatory green sunfish, Lepomis cyanellis. In these streams the optimal larval strategy entails reduced activity level to remain inconspicuous and avoid predation (Sih, et al. 1988; Kats, et al. 1988). In other shallow streams, a key selection pressure is habitat ephemerality, where the optimal larval strategy entails increased activity level to feed rapidly in order to reach a large enough size to metamorphose before the stream dries up (Petranka and Sih 1987). Recent work has shown that gene flow is high enough between these two population types to swamp local adaptation (Storfer, unpublished data). Additional data indicate that this gene flow has caused adaptation to the average of local conditions because a number of behavioral (i.e., refuge use, escape response) and life history assays (i.e., stage at hatching) associated with predator avoidance have been shown not to differ significantly between two populations (one with fish, the other ephemeral) connected by gene flow (Storfer, unpublished data). Even so, isolated populations do differ significantly in those traits associated with fish avoidance. Therefore, gene flow may be swamping local adaptation in some populations of A. barbouri and making them potentially more susceptible to fish predation.

Management implications

Gene flow can play a major role in the management of threatened or endangered species. In particular, it is important for conservation biologists and resource managers to gain a better understanding of gene flow as a constraining force. That is, there is

enough uncertainty about whether gene flow acts as a disrupter of local adaptation to warrant caution toward management plans that include the enhancement of interpopulation connection and gene flow. Gene flow can be a particularly important issue for amphibian species. For example, salamanders have typically low levels of gene flow, thus making populations naturally subdivided (Larsen et al. 1984; Slatkin 1985). Enhancement of gene flow for conservation purposes may therefore not be warranted based upon the fact that natural historical associations may not exist between the populations. It is therefore important to conduct more studies of gene flow in amphibian and reptile species, especially since techniques of measuring gene flow have become more and more accessible (see Slatkin 1985). Studies of gene flow provide insight into population structure and historical associations between populations helping resource managers to avoid mixture of populations without high levels of gene flow, exhibited by many amphibians species in nature.

It is essential to conduct ecological surveys of habitat types and major selection pressures that affect species which are management candidates, such as limiting resources (*i.e.*, prey, space, nest sites, etc.), major predators, and intrinsic habitat differences (*i.e.*, climatic differences). These brief surveys would not slow critical conservation decisions, yet they would provide extremely valuable information so that populations that are most ecologically alike could be those that are mixed (when such management may be warranted). Without such data, resource managers cannot be sure that mixing populations will not negatively affect the very populations that they are trying to save.

References

Camin, J. and Ehrlich, P. 1958. Natural selection in water snakes, $(Natrix\, sipedon\, L.)$ on islands in Lake Erie. $Evolution\, 12:\, 504-511.$

Frankel, O.H. and Soulé, M.E. 1981. Conservation and Evolution. Cambridge University Press. Cambridge, United Kingdom. 327 pp.

Greig, J.C. 1979. Principles of genetic conservation in relation to wildlife management in South Africa. South African Journal of Wildlife Restoration 9: 57-78.

Kats, L.B., Petrauka, J.W., and Sih, A. 1988. Antipredator responses and the persistence of amphibian larvae with fishes. Ecology~69:~1865-1870.

King, R.B. 1993a. Color pattern variation in lake Erie water snakes: Prediction and measurement of natural selection. *Evolution* 47: 1819-1833.

King, R.B. 1993b. Color pattern in lake Erie water snakes: Inheritance. Canadian Journal of Zoology 71: 1985-1990.

King, R.B. 1992. Lake Erie water snakes revisited: Morph and age specific variation in relative crypsis. *Evolutionary Ecology* 6: 115-124.

King, R.B. 1987. Color pattern polymorphism in the lake Erie water snake, *Nerodia sipedon insularium*. Evolution 41: 241-255.

Lande, R. 1988. Genetics and demography in biological conservation. *Science* 241: 1455-1460.

Lande, R. and Barrowclough, G.F. 1987. Effective population size, genetic variation, and their use in population management, pp. 87-125 in Soulé, M.E. (editor). *Viable Populations for Conservation*. Cambridge University Press, Cambridge, United Kingdom. 189 pp.

Larsen, A., Wake, D.B., and Yanev, K.P. 1984. Measuring gene flow among populations having high levels of genetic fragmentation. *Genetics* 106: 293-308.

Mayr, E. 1963. Animal Species and Evolution. Harvard University Press, Cambridge, Massachusetts. 797 pp.

Mayr, E. 1969. *Principle of Systematic Zoology*. McGraw-Hill, New York, New York. 428 pp.

Petranka, J.W. and Sih, A. 1987. Habitat duration, length of the larval period and the evolution of a complex life cycle of an amphibian. *Evolution* 41: 1347-1356.

Schemske, D. *et al.* 1994. Evaluating approaches to the conservation of rare and endangered plants. *Ecology* 75: 584-606

Sih, A., Petranka, J.W., and Kats, L.B. 1988. The dynamics of prey refuge use: a model and tests with sunfish and salamander larvae. *American Naturalist* 132: 463-483.

Slatkin, M. 1985. Gene flow in natural populations. *Annual Review of Ecology and Systematics* 16: 393-430.

Slatkin, M. 1987. Gene flow and the geographic structure of natural populations. *Science* 236: 787-792.

Templeton, A.R. 1986. Coadaptation and outbreeding depression, pp. 105-116 in Soulé, M.E. (editor). Conservation Biology: The Science of Scarcity and Diversity. Sinauer Associates, Sunderland, Massachusetts. 584 pp.

Wright, S. 1951. The genetical structure of populations. Annals of Eugenics 15: 323-354.

After a brief stint as a Fish and Wildlife Biologist for the US Fish and Wildlife Service in 1992, Andrew Storfer began work as a graduate student in the Center for Ecology, Evolution and Behavior at the University of Kentucky. Since that time, he has been studying the evolutionary effects of gene flow in a stream-dwelling salamander that is endemic to Kentucky. His research incorporates aspects of genetics, population ecology and behavior in an unusually integrative project. Andrew expects his Ph.D. in May of 1997.