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# Gene flow and endangered species translocations: a topic revisited

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## Abstract

Understanding the evolutionary role of gene flow is pivotal to the conservation of endangered populations. Gene flow can be enhanced through population translocations that are conducted to maintain genetic variation and combat the negative consequences of inbreeding depression (two of the major concerns in the conservation of subdivided or isolated populations). While researchers have given extensive consideration to the idea that gene flow can act as a creative evolutionary force by maintaining genetic variation or spreading adaptive gene complexes, the focus of this paper is to investigate gene flow as a force that constrains local adaptation. I briefly review the theoretical basis of and summarize empirical studies that indicate gene flow can constrain local adaptation, and may thereby lower short-term population fitness. This review suggests that knowledge of gene flow rates and understanding ecological differences among populations is necessary before embarking on a program to artificially enhance gene flow. © 1998 Elsevier Science Ltd. All rights reserved.

*Keywords:* Gene flow; Endangered species; Translocations; Captive breeding

## 1. Introduction

Understanding the evolutionary role of gene flow, or migration of individuals and the subsequent transfer of genes among populations, is pivotal to the management of endangered species (Frankel and Soulé, 1981; Real, 1994; Soulé, 1986; Vrijenhoek, 1989). Moderate to high rates of gene flow among populations help prevent subpopulation isolation, thereby maintaining genetic variation and preventing inbreeding depression (Franklin, 1980; Frankel and Soulé, 1981). Habitat fragmentation can restrict gene flow, which can result in the loss of genetic variation. As a result, management strategies often include translocations among populations or captive breeding and release of individuals into natural populations. Whether these programs directly consider the effects of gene flow, they act to enhance gene flow among populations (Avise, 1994). Implicit in these management designs is the assumption that gene flow will have positive effects by acting as a creative evolutionary force in maintaining genetic variation and/or introducing favorable migrants (i.e., well-adapted

individuals with high fitness; Wright, 1931; Slatkin, 1987). However, gene flow can also act as a force that constrains local adaptation (Slatkin, 1987). Genetic mixture of populations that are adapted to different local conditions can result in outbreeding depression, the reduction in fitness caused by the breakdown of coadapted gene complexes (Shields, 1982; Templeton, 1986). Gene flow is also thought to swamp local adaptation in populations with conflicting selection pressures (Templeton, 1986; Slatkin, 1987). Moreover, long-term genetic mixture among populations with different selection regimes can preclude the evolutionary development of new species (Mayr, 1963, 1969 and 1970).

The purpose of this paper is to review studies which show that gene flow can constrain local adaptation and thus impact the management of endangered populations. I present a brief background on the theoretical basis for enhancing gene flow as a tool for management of endangered populations. Then, I review empirical work demonstrating that gene flow can be a force constraining adaptive evolution and cases where human enhancement of gene flow has failed to augment populations or appears to be causing a population decline. Finally, I present management recommendations to address the problem of altering gene flow in conservation programs.

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### 1.1. Gene flow and conservation: basic background

“Recognizing the genetic diversity that exists among migrants seems essential when constructing policies for reintroducing or augmenting declining populations of important species...” (Real, 1994 p. xiv).

The loss of genetic diversity is a central topic in conservation genetics (Avice, 1994). Small populations are prone to inbreeding, which causes reduction of heterozygosity, and genetic drift, which can result in the loss of allelic diversity. In the short-term, a reduction in population fitness can result from inbreeding and the consequent reduction of heterozygosity in small populations (Quattro and Vrijenhoek, 1989; Vrijenhoek, 1994). Inbreeding can act to unmask recessive deleterious alleles, also lowering population fitness (Ralls and Ballou, 1983; Ralls et al., 1986; Ledig, 1986; Charlesworth and Charlesworth, 1987; Quattro and Vrijenhoek, 1989; Lacy, 1992; Jiminéz et al., 1994). Conservation biologists are additionally concerned that declines in genetic variation may inhibit the future ability of an organism to adapt to environmental change and consequently limit its evolutionary potential (Franklin, 1980; Frankel and Soulé, 1981; Soulé and Gilpin, 1986; Vrijenhoek, 1989).

Translocation of individuals from larger populations (which tends to increase gene flow) can be used to supplement genetic variation in small populations, thereby reducing the possibility of inbreeding depression and the loss of genetic variation (see Lande and Barrowclough, 1987; Stockwell et al., 1996). Yet, the number of individuals to translocate remains unclear. For some time, managers used the ‘one-migrant-per-generation’ rule as a guideline (Mills and Allendorf, 1996). The theoretical basis for this decision goes back to Wright (1931), who calculated that one breeding migrant per generation is sufficient to prevent subpopulation differentiation by drift alone (in neutral alleles); this result was supported by later models as well (for reviews see Felsenstein, 1976; Slatkin, 1985). Allendorf (1983) suggested this rate allowed populations to overcome drift while still allowing for local adaptation among demes.

However, the one-migrant-per-generation rule is based upon several assumptions that may be unrealistic in endangered populations. One important assumption in Wright’s (1931) model is that populations are in equilibrium of migration (gene flow) and drift. Varvio et al. (1986) questioned whether small, declining populations are in equilibrium at all. For example, endangered species with frequent local colonizations and extinctions may either increase or decrease the number of migrants necessary to prevent drift (Mills and Allendorf, 1996). Equilibrium between gene flow and drift is reached more quickly in small populations than larger ones, so knowledge of population size is important (Allendorf and Phelps, 1981; Mills and Allendorf, 1996).

Wright’s model also assumes demographic equality of migrants. Immigrants may often count as less than one migrant because translocated individuals may not mate and become part of the gene pool (Endler, 1977). Aliens are often unfamiliar with the habitat and may be ostracized in social species; consequently, their probability of successful matings is reduced (Endler, 1977). The number of individuals appropriate for introduction is also likely to be temporally variable because the individuals that comprise the breeding population change through time.

Other assumptions, such as effective population size is equal to census population size, are most likely violated in endangered populations. For census size to be equal to effective population size there must be equal numbers of breeding males and females and population size must be temporally constant (see Lande and Barrowclough, 1987). Violations of these assumptions tend to increase the number of migrants necessary to prevent subpopulation allelic differentiation (Mills and Allendorf, 1996).

Consequently, the widely accepted value of ‘one migrant per generation’ may be based upon assumptions that apply in only limited circumstances, and led Mills and Allendorf (1996) to suggest that a minimum of one and a maximum of 10 migrants per generation are appropriate for management purposes. The authors argue that such levels will prevent subpopulation differentiation but will still allow for local adaptation among demes.

How much gene flow is enough to swamp local adaptation depends on the magnitude and direction of selection in the interacting populations (Shafer, 1990). Wright (1931) predicted that greater than four migrants per generation is sufficient to cause population panmixis, or complete genetic mixture. Models of gene flow and selection generally demonstrate that beyond some threshold, gene flow is likely to homogenize interacting populations (Haldane, 1930; Slatkin, 1985, 1987). In general, if the selection coefficient ( $s$ ) is less than the migration rate ( $m$ ), then selection will not have an appreciable effect on allele frequency divergence among populations. However, if there are large selective differences among populations (i.e.  $s > m$ ), then selection will cause allele frequency divergence. Subsequent artificial augmentation of gene flow may homogenize this divergence, particularly in small, isolated populations where  $m$  is expected to be low. Ecological knowledge of candidate populations would therefore help narrow this broad range.

In some circumstances, it may be advantageous to maintain or even foster population subdivision instead of translocations that increase gene flow. The maintenance of several isolated populations can actually increase overall genetic diversity because allelic differences can be preserved due to local adaptation to different

habitats (Mayr, 1942, 1969; Endler, 1977). Also, the random effects of genetic drift will tend to fix different alleles in different populations, and overall allelic diversity may be preserved in the total group of subpopulations (Chesser, 1983). Population subdivision is also necessary for the shifting balance process to occur, which ultimately results in increased population fitness (Wright, 1931, 1988). Populations with conflicting selection pressures may be good candidates for the maintenance of population subdivision. In such cases, researchers should weigh the potential for inbreeding depression or the loss of alleles due to drift against the possible consequences of outbreeding depression.

In the following sections, I discuss the effects of species translocations with focus on: (1) translocation of individuals between existing natural populations; and, (2) captive breeding programs that include either reintroductions of populations into regions from which they have been extirpated, or restocking of existing wild populations to bolster both effective population size and genetic variability.

### 1.2. Translocations

Translocations include both the artificial movement of individuals between natural populations and the release of (often captive-reared) animals to reintroduce or augment a population. Translocations have been widely proposed for, or utilized in conservation programs to alleviate the detrimental effects of inbreeding depression and demographic stochasticity (Allendorf and Leary, 1986; Simberloff and Cox, 1987; Lande and Barrowclough, 1987; Simberloff, 1988; Griffith et al., 1989; Beck et al., 1994; Stockwell et al., 1996). Several criteria have been associated with successful translocation. These include, habitat quality, where species are released relative to the extent of their range (i.e. center, periphery or outside), and whether animals were wild-caught or captive-reared (Griffith et al., 1989). In general, translocations have been variable in their success. The following review focuses on the potential effects of gene flow as an underlying mechanism in failed translocations.

Translocated populations can hybridize with native populations of the same species or closely related species, consequently impacting the genetic purity of each species. An example is the introduction of the Sika deer (*Cervus nippon*) to Western Europe. Sika deer readily interbreed with native red deer (*C. elaphus*) and as a result, there are no pure red deer remaining in parts of Great Britain (Lowe and Gardner, 1975). Several other examples of such introgression are cited in Greig (1979).

Translocations can also have detrimental consequences for population fitness. For example, hybridizing populations from different latitudes can result in a sub-optimal breeding time with the consequent birth of offspring

when resources are scarce. Greig (1979) emphasized the importance of different photoperiods experienced by populations at different latitudes. Photoperiod often determines the times at which species are receptive to mating, which leads to synchronization of birth and resource availability (Sadleir, 1969). Crossing populations with different photoperiods can thus lead to reduced offspring survival, as was the case with the translocation of feral goats from the Mediterranean to Wales (Greig, 1979).

Other translocations have reduced resident population fitness due to introgression of poorly adapted gene complexes. Bobwhite quail (*Colinus virginianus*) were translocated from the southern United States to augment the Ontario game population. However, the hybrid quail were less able to survive the northern winters, and the population declined (Clarke, 1954). Carr and Dodd (1983) reported that Ascension Island green sea turtles (*Chelonia mydas*) weighed significantly more than the conspecific Atlantic population. They suggested that this difference was associated with fat storage needed for the 3500 kilometer island turtle breeding migration. Hybridizing the two populations has been suggested because it could result in increased fitness due to hybrid vigor. However, Carr and Dodd (1983) cautioned against interbreeding the island and Atlantic populations because hybrids may not reach a large enough size to migrate and breed.

Translocated populations may simply not be well adapted to the area in which they are introduced. Bighorn sheep (*Ovis canadensis*) that were translocated from Canada to Oklahoma died out because of the dramatic shift in climate conditions (Halloran and Glass, 1959).

Translocations can also result in the transmission of disease (Cunningham, 1996). Samuel et al. (1992) warn that the translocation of elk (*Cerphus elaphus*) may also result in the transmission of a parasitic meningeal worm. Without readily usable protocol for diagnosis of infestation, translocation of elk may result in reduced population fitness, rather than the goal of augmenting populations (see Ballou, 1993; Cunningham, 1996).

Another concern is that translocations may result in dystocia, or difficult parturition, in some species (Galindo-Leal and Weber, 1994). Dystocia can be caused by crossing animals that are differently sized or proportioned, and it has resulted in perinatal calf losses or death of the mother in both cattle and sheep (Jainudeen and Hafez, 1987). For this reason, it is important to introduce animals that are similarly sized to native animals.

### 1.3. Gene flow from captive stocks

Captive breeding programs usually have at least one of three major goals: (1) reintroduction of critically

endangered or extirpated populations; (2) bolstering effective population size and genetic variation of existing populations; and (3) adding individuals to economically important, yet declining game species' populations. Captive breeding, however, can result in detrimental genetic effects in the captive populations, such as: inbreeding depression, the loss of genetic variability via genetic drift, or domestication selection (Lacy, 1987; Allendorf, 1993; Snyder et al., 1996). The concern is that these genetic problems may be introduced (via gene flow) into natural populations when captive animals are released.

Inbreeding depression, has recently been documented in captive wolf (*Canis lupus*) populations (Laikre and Ryman, 1991). Ralls and Ballou (1983) review the effects of inbreeding in zoo animals; in almost all instances, they found juveniles from inbred lines had higher mortality rates than non-inbred progeny.

An additional problem is domestication selection, or artificial selection imposed by the captive environment. Domestication selection may be almost unavoidable, because initial population sizes are typically small enough that several generations of captive breeding are necessary to reach a large enough population size for viable reintroduction. Captive individuals then have the possibility of introducing deleterious genes and reducing the fitness of wild populations when they are reintroduced (Fleming and Gross, 1993; Snyder et al., 1996). For example, behavioral deficiencies documented in captive populations (see Miller et al., 1990; Wiley et al., 1992; Fleming and Gross, 1993; Snyder et al., 1996) could cause unsuccessful introduction or be transmitted to wild stocks through hybridization.

Several examples exist where captive populations have caused or may cause unfavorable introgression into wild populations. Captive stocks of the coho salmon (*Oncorhynchus kisutch*) have been shown to have significantly lower rates of survival and reproductive success than wild coho salmon after only seven generations of artificial selection for the rearing pond-type environment (Fleming and Gross, 1993). The rearing ponds select for an aggressive-feeding phenotype, which would be selected against in natural streams due to increased exposure to predators (Fleming and Gross, 1993). If captive-reared fry reach sexual maturity and breed with native salmon, they may actually decrease the fitness of natural stocks due to increased predation. Similarly, captive-raised sea turtles have low fertility rates and will likely hybridize with wild populations if they are introduced; this may result in lower fertility of wild individuals (Carr and Dodd, 1983). In addition, hatchery trout (*Salmo trutta*) failed to reach sexual maturity, so their introduction failed to augment natural populations in Spain (Moran et al., 1991). Several other examples of genetic introgression, hybridization, and population decline in natural stocks have occurred

with the introduction of captive-reared fishes (Martin et al., 1985; Hindar et al., 1991; Pastene et al., 1991; Meffe, 1992; Allendorf, 1993; Hayes et al., 1996). For the above reasons, it is important to make the captive environment as realistic as possible and to minimize the number of generations that captive populations are artificially selected.

In general, introductions from captive-bred lines have had half the success rate of translocations of wild-caught individuals, which indicates that captive breeding can compromise the survival of reintroduced populations (Griffith et al., 1989). In a more recent review of 145 reintroductions, only 16 were successful in establishing wild populations (Beck et al., 1994).

#### 1.4. Gene flow as a constraining force—natural examples

The conditions under which gene flow can constrain local adaptation have been investigated with considerable mathematical work (Slatkin, 1987). A growing body of empirical work in natural populations also provides support for this idea.

In one of the first studies that considered the constraining effects of gene flow in natural populations, Camin and Ehrlich (1958) examined color pattern variation in Lake Erie island and mainland water snakes (*Nerodia sipedon*). Banded snakes were more cryptic (and much more common) in the wooded areas of the mainland while unbanded snakes were more common and more cryptic in the open, rocky areas of the islands. Varying degrees of banding were found over several years in the juvenile island populations, despite its selective disadvantage (this color morph was more easily detected by predators). Gene flow has since been measured in these snake populations with isozyme techniques, and was found to be high enough to maintain the observed polymorphism on the islands (King, 1987). Thus, it was determined that gene flow from the mainland population was overwhelming the effect of selection, which caused an observed decline in population fitness (King, 1987; King and Lawson, 1995).

Kettlewell (1956) initiated the classic series of studies on the pepper moth (*Biston betularia*) in Great Britain. Pepper moths are so named because of their polymorphism of color; light moths are most common in rural areas, where tree trunks are white, and dark (melanic) moths are found in industrial areas, where tree trunks are black. However, Kettlewell consistently found melanics in rural areas and light colored moths in industrial areas despite strong selection by bird predators that should eliminate non-camouflaged morphs. Bishop and Cook (1975) added experiments that confirmed Kettlewell's initial results. They sampled moths at over 100 sites and continually found a small percentage of moths that were not camouflaged to their

habitat. Because a mark-recapture experiment indicated that most moths traveled over a kilometer, the authors suggested gene flow between the populations caused the observed reduction in population fitness.

Stearns and Sage (1980) later investigated the apparent maladaptation of the mosquito fish (*Gambusia affinis*) in two populations. One population was in a brackish estuary and the other in a series of freshwater pools that ranged from 150 to 300 m away. Initial observations indicated that freshwater females had significantly fewer young and invested less reproductively than females from the brackish population. Mated females were then brought into the lab and broods were raised in both brackish and fresh water treatments. Regardless of the mother's origin, offspring differed significantly in their survival to 86 days of age (51.5% in fresh water and 93.5% in brackish). These results indicated that mosquito fish were apparently less well adapted to the freshwater pools. An electrophoretic survey indicated that there was detectable gene flow between the two populations. The authors suggested that this continued gene flow may have acted to inhibit local adaptation in the freshwater population.

Waser and Price (1989) found that the optimal outcrossing distance in the scarlet gilia (*Ipomopsis aggregata*) was 10 m. They found that lifetime fitness declined 50% in offspring that resulted from self-fertilization and over 30% in crosses of plants over 100 meters apart when compared with this distance. Here, they demonstrated both inbreeding and outbreeding depression, and consequently found that an intermediate rate of gene flow is optimal. Svensson (1990) supported this result with data in populations of *Scleranthus annuus*, showing a 19–36% decline in male fertility in matings that were 75–100 meters apart versus matings at a distance of 6 m.

Dhondt et al. (1990) demonstrated that gene flow between local populations of great tits (*Parus major*), and blue tits (*Parus cereuleus*) with different habitat quality was the likely cause of the production of non-optimal clutch sizes. The authors used theory to predict that clutch sizes should be larger in good quality habitats than in poor habitats. However, actual clutch sizes did not differ among habitat types (i.e. tits produced clutches that were too small in good quality sites and too large in poor quality sites). A large majority of breeding birds were migrants from other sites; thus gene flow appeared to be a homogenizing force that constrained local adaptation among different quality habitats for both species (Dhondt et al., 1990).

Riechert (1993) found dramatic differences in the foraging and antipredator behaviors in two populations of the desert spider (*Agelenopsis aperta*). Spiders showed a low discrimination of prey profitability in a riparian population where prey were abundant. This was an apparent 'maladaptation', because optimal diet models

predict that foragers should be highly selective in areas with abundant prey. Gene flow was extremely high and unidirectional from a nearby desert population, where prey were scarce and spiders should show lower prey discrimination than those in the riparian population. When Riechert (1993) prevented gene flow for one generation, riparian spider behavior shifted dramatically toward the optimal phenotype. It was concluded that gene flow from the desert population inhibited local adaptation in the riparian spider population (Riechert, 1993).

My recent work supports gene flow as a constraint to local adaptation in larvae of the streamside salamander (*Ambystoma barbouri*) that have conflicting selection pressures in different streams (Storfer and Sih, 1998). Some streams support predatory fish, where the optimal larval strategy is to reduce activity level and hide under refuge (Sih et al., 1988, 1992). But, in other fishless streams habitat ephemerality promotes increased larval activity to feed rapidly to metamorphose before the stream dries up (Maurer and Sih, 1996). Gene flow between the two habitat 'types' appears to cause some salamander larvae in streams with fish to be 'overactive' and suffer high rates of predation; the strength and effectiveness of antipredator behavior in populations with fish is directly related to the genetic isolation of the population from its nearest fishless neighbor (Storfer and Sih, 1998).

Some studies have shown that gene flow apparently acts to oppose local selection in allozyme polymorphisms. An early example of this work was done on a marine mussel (*Mytilus edulis*). Koehn et al. (1983) showed that the mussel is polymorphic for the aminopeptidase I allele, with one particular form of the enzyme (Lap<sup>94</sup>) having 20% higher activity than the two other alleles (Lap<sup>96</sup> or Lap<sup>98</sup>). While Lap<sup>94</sup> may be beneficial in marine habitats with high salinity, the allele is also found in estuarine populations, where individuals show higher mortality and poorer physical condition than individuals with either of the other two alleles (Koehn et al., 1983). Dispersal (gene flow) was inferred as the mechanism to maintain the relatively high frequency of Lap<sup>94</sup> in estuarine populations, despite opposing local selection (Koehn et al., 1983). More recently, Ross and Keller (1995) showed that gene flow acts to oppose local selection for the Pgm-3 enzyme in fire ants (*Solenopsis invicta*). In one population, worker ants destroy queens (before they reproduce) that are homozygous for *Pgm-3<sup>a/a</sup>*, which creates strong negative selection against the *Pgm-3<sup>a</sup>* allele (Ross and Keller, 1995). Gene flow from another population with a different social form, where the allele is common and no selection opposing it was found, acts to maintain the allele in the population where selection opposes it. It is perhaps these studies that provide some of the strongest evidence for gene flow as a constraint to adaptive evolution because they show that gene flow maintains

frequencies of specific alleles that are higher than expected under selection (see also Macnair, 1981).

### 1.5. Summary of empirical studies

Gene flow has been shown to be a constraining force in several natural, unmanipulated populations of various vertebrates, plants, and some invertebrate species. In cases of managed populations, the two mechanisms that resulted in increased gene flow were most often species translocations or captive breeding and release of individuals into existing populations. Of translocations or captive breeding-reintroduction attempts that failed, common reasons included outbreeding depression and genetic introgression from captive stocks that underwent domestication. Few studies have considered the potential negative consequences of outbreeding and gene flow at all (for examples see Vrijenhoek, 1994; Hedrick, 1995).

## 2. Summary

Understanding the evolutionary role of gene flow has been a major theme in the field of population genetics and should be considered important in making conservation decisions. The research cited in this paper shows that gene flow is important in the management of threatened and endangered species and that conservation biologists and resource managers need to give more consideration of gene flow as an evolutionarily *constraining* force.

## 3. Management recommendations

1. When the artificial enhancement of gene flow is proposed, the historical relationships of the managed populations should be considered for three main reasons. First, biologists may mix populations with no historical connection, and thereby homogenize prior subpopulation differentiation. This may serve to swamp local adaptation and/or homogenize fixed genetic differences. Second, continued introgression may prevent future local adaptation. Third, our inability to predict future environmental change presents a problem with enhancing gene flow. Continued introduction of populations that are poorly adapted may prevent future local adaptation.
2. Biologists should conduct more studies of gene flow because techniques of estimating gene flow have become more accessible (see Slatkin, 1985; Slatkin and Barton, 1989; Avise, 1994). These studies provide insight into population structure, a species' colonization ability, and its evolutionary

potential. Although time is of the essence in creating management schemes for endangered species, rapid assessments of gene flow may be attainable. Allozyme techniques may be useful and are relatively quick and inexpensive (Hamrick et al., 1991). However, allozymes may not yield enough variation to determine population-level substructure in endangered species. New techniques and theory now make it possible to estimate gene flow from differences in DNA sequences (Slatkin and Maddison, 1989; Slatkin, 1993), and automated DNA sequencers are making such data more easily obtainable. Recent theory allows researchers to test whether population-level differences are a result of current or historical genetic associations between populations (Templeton et al., 1995). These data might be especially important so researchers can translocate populations with the closest historical associations. Gene flow and population substructure can also be estimated with the use of mini- or microsatellite markers, which are hypervariable tandem DNA repeats. These markers are initially difficult to develop, but more and more markers are being developed for a greater number of species. As primers for these markers become more readily available, they may be useful in future genetic studies of endangered species.

3. Finally, it is essential to conduct ecological surveys of habitat types and major selection pressures that affect different populations of endangered species. These studies should yield insight into which populations are the most similar ecologically, and therefore, which populations would be appropriate for enhancement of gene flow.

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