

Species Conservation and Natural Variation Among Populations

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Modifications of the phenotype that do not involve genetic changes have long been considered...to lack evolutionary significance. This view is not correct.

- Ernst Mayr

Introduction

In conservation planning, the importance of natural variation is often given inadequate consideration. However, ignoring the implications of variation within species may result in conservation strategies that jeopardize, rather than conserve, target species (see Grieg 1979; Turcek 1951; Storfer 1999). Natural variation in the traits of individuals and populations is the product of the genetic composition of the individual and the environment to which the individual is exposed. Inherited traits are those that are largely genetically determined, whereas non-inherited traits result primarily from environmental influences and are not under *direct* genetic control. Inherited and non-inherited traits are an oversimplification of a complex phenomenon and represent two ends of a gradient of variation.

Natural variation exists within and among populations. It is unwise to assume that behavioral or genetic attributes exhibited by one population are within the range of behavioral or genetic potential of another (Ruggiero et al. 1988). When this assumption is false, it can result in failed reintroduction efforts or a net loss of genetic or behavioral variability (e.g., Halloran and Glass 1959 and examples provided in Storfer 1999). Similarly, problems can also result from applying ecological knowledge from one population to the conservation needs of other populations inhabiting substantially different habitats.

In this chapter, we review fundamental concepts related to patterns of natural variation in populations and discuss their relevance to the process of species conservation. First, we define some of the terms used in this chapter and discuss how geographic variation in environmental conditions may lead to variation among populations. We then discuss differences between inherited and non-inherited variation and the role each may play in structuring populations within species. Lastly, we discuss the implications of natural variation among populations to lynx conservation.

We use the following terms and concepts: *genotype* refers to a particular set of genes possessed by an individual, and *phenotype* is the outward appearance and behavior of the individual (Ricklefs 1990), which is determined by interactions between the genotype and the environment. *Phenotypic plasticity* is the capacity for a single genotype to produce multiple phenotypes,

often as the result of varying environmental influences (Falconer and Mackay 1996). *Adaptation* is a trait that permits an organism to function well in its environment and endows it with capabilities especially appropriate for its particular environment (Roughgarden 1979).

Within- and Among-Population Variation

Populations and Species

Natural variation exists between individuals in a population and between populations of a species. A *population* is a group of conspecific organisms living near enough to one another that both ecological and reproductive interactions occur more frequently within the group than with members of other populations (Futuyma 1986). Populations are composed of unique individuals possessing varying behavioral and physical traits, and can only be characterized by the range of variation in these traits. Variation also exists among populations within a species (Endler 1986; Lott 1991). Differences among populations generally increase with distance and / or isolation.

In general, the aggregation of these populations comprises a species (for more specific definitions of the species see reviews in Futuyma 1998; Mallet 1995). Therefore, a species encompasses variation occurring both within and among populations. Species are not composed of uniform, interchangeable populations; they are more like jigsaw puzzles with many unique pieces.

Species Range and Dispersal Capability

Diversity among populations can be reduced when a species' dispersal capability is great relative to the spatial extent of its range, and when barriers do not impede dispersal or gene flow (Mills and Allendorf 1996; Wright 1969). However, in widely distributed species, such as the lynx, distance alone can function as a barrier to genetic exchange among populations, even when individuals are capable of long-distance movements. This is known as *isolation by distance* (see Britten et al. 1995; Hartl and Clark 1989; Wright 1943). Physical features of geography and habitat may also act as both absolute and psychological barriers to movements and dispersal (e.g., Buskirk and Ruggiero 1994; Diamond 1975; Mayr 1970) and impede gene flow. Thus, dispersal and gene flow are not simply mechanical processes governed by a species' movement capabilities, they are also affected by geographic influences on the movements of individuals, behavioral responses to perceived barriers, and the probability of successful reproduction in new environments.

Central vs. Peripheral Populations

Central populations are usually large, continuous, and occupy favorable habitats. Peripheral populations, by contrast, can be more or less isolated, fragmented, and subject to a more variable physical environment (Carson 1959; Lesica and Allendorf 1995). Accordingly, peripheral populations will often experience different selection pressures than central populations, which may lead to genetic divergence (but see Kirkpatrick and Barton 1997).

Differences in genotype and phenotype are most likely to occur in populations that have become isolated at the periphery of the range (Lesica and Allendorf 1995; Mayr 1970; Safriel et al. 1994). Isolated populations lack or have greatly reduced levels of immigration and, consequently, may diverge from central populations due to genetic drift and natural selection. Peripheral populations often have reduced levels of genetic variability relative to central populations (Lesica and Allendorf 1995)

Genes vs. Environment: A False Dichotomy

Assessments of natural variation among populations are generally focused on traits that have a direct genetic basis (i.e., inherited traits), with little emphasis on those that do not (e.g., Vogler and DeSalle 1994). The prevailing view seems to be that because only genetic material is inherited, it represents the essential element of natural variation, selection, and adaptation. In contrast, a phenotype for which no direct genetic basis is known is thought to be of less evolutionary significance and of only minor importance in conservation planning (see Pennock and Dimmick 1997; Rohlf 1994). However, we believe this view to be fundamentally incorrect because phenotypic plasticity (which is itself a genetic trait) and its effects on individual fitness can play a key role in evolutionary processes (Mayr 1970; Pianka 1994).

Natural Selection and Inherited vs. Non-inherited Traits

Evolutionary theory states that populations contain inherited variation that arises by random mutation and recombination and which is acted upon by random genetic drift and natural selection. Natural selection is the differential reproductive success of different phenotypes, a process which slowly changes gene frequencies in populations. Those individuals with phenotypes that are selected against are less successful than others and, eventually, their genes are eliminated from the population.

Traits that are largely influenced by the environment are considered non-inherited. This does not mean that these traits are non-genetic. Most non-inherited traits are under “indirect” genetic control, as it is ultimately the

genes of the individual that allow the phenotype to be shaped by the environment. When natural selection acts upon these phenotypes, gene frequencies do not immediately change because there is no direct correlation between the genotype and the phenotype. However, non-genetic modifications of the phenotype that occur in the absence of genetic change can be adaptive, can influence fitness, and may be preserved by indirect genetic mechanisms and learned behaviors (Falconer and Mackay 1996; Grant 1963; Mayr 1970).

The evolutionary significance of phenotypic plasticity has been discussed in many contexts (Baldwin 1896; see also Ancel 1999 and Simpson 1953). Baldwin argued that such responses might permit a population to inhabit an environment to which it is poorly adapted. Through this mechanism, the population may gain the time necessary to acquire, through mutation, genotypes with an adaptive advantage (Grant 1963).

Discriminating between inherited and non-inherited traits is extremely difficult. To determine if a behavioral, physiological, morphological, or biochemical trait is strongly influenced by the environment requires careful laboratory study (e.g., common garden and reciprocal transplant experiments). Such studies are nearly impossible with large, highly mobile organisms like the lynx.

Examples of Strong Environmental Influences on Phenotypic Traits

There are many classic examples of natural selection acting upon heritable traits (e.g., Boag and Grant 1981; Reznick et al. 1990). There appear to be fewer instances where the local environment has been shown to determine a phenotype. In this section, we review several cases where environment plays a large role in shaping the phenotype.

Rhymer (1992) conducted both a reciprocal transplant and a common-garden experiment with mallards from California and Manitoba to see if size variations were inherited. She found that while some differences in the size and morphology of mallards persisted regardless of environment, most of the variation in size was under environmental control. Growth in ducks is not locally adapted as was previously suggested (Lightbody and Ankeny 1984), but was determined by local environmental conditions at the time of rearing (Rhymer 1992).

Red-winged blackbirds show large clinal variation in size and shape. James (1983) conducted a reciprocal transplant experiment with red-winged blackbird eggs from northern and southern Florida and a single transplant experiment from Colorado to Minnesota. She concluded that regional variation in the shape of red-winged blackbirds was largely non-genetic because

transplanted eggs produced birds more like the phenotypes typical of their adopted area.

Geist (1991) discussed the taxonomic status of wood bison that were previously thought to be a subspecies distinct from the plains bison. He concluded that observed differences between plains and wood bison were not genetically determined, but were phenotypic differences associated with diet. Thus, differences between wood bison populations appear to be based on phenotypic plasticity.

Learned behaviors also demonstrate the strong influence of the local environment on a trait. Both within and among populations, individuals can exhibit a wide range of learned behaviors. The inheritance of learned behavior is termed *cultural inheritance* (Cavalli-Sforza and Feldman 1973). A well-known example is the learned ability of several species of British birds to open milk bottles. This behavior was first reported in the 1920s and Hinde and Fisher (1951) have subsequently mapped its spread over an extensive area. Recent work by Lefebvre (1995a) indicates that the spread of milk-bottle opening by birds has been accelerating across the United Kingdom (U.K.). However, the behavior is still not found in some U.K. populations, even though it is prevalent in others.

Cultural inheritance has also been reported in primates (see Lefebvre 1995b). Kawamura (1954) noted that neighboring troops of Japanese macaques differed in feeding habits, and others began feeding the macaques to observe their social behavior. One of the foods they provided was wheat grains spread on a sandy beach, a food source that was difficult for the monkeys to handle. One female macaque separated out the wheat grains, which floated, by placing handfuls of sand into puddles of water on the beach. Shortly thereafter, researchers saw other troop members imitate the separation technique (Kawai 1965). Soon, it became a technique unique to members of this troop and not found in other troops.

The key point is that non-inherited traits are often adaptive and therefore can influence fitness and evolution. Accordingly, phenotypic variety must be carefully considered by conservationists regardless of the mechanism by which it was created.

Considerations for Conservation Planning

Reintroductions, Augmentations, and Translocations

Reintroduction entails moving individuals from one or more wild populations to parts of the species' range where local populations no longer exist. Population *augmentation* is the process of moving individuals from one or

more wild populations to a different part or parts of the species' range where local populations are precariously small. We refer to any relocation of individuals from an existing wild population into a new environment as a *translocation*.

Augmenting populations with captive-bred animals, or introducing captive-bred individuals into the wild, is generally problematic. Captive-bred animals usually have lower survival rates, a reduced fright response to predators, and may lack other behaviors necessary to survive in the wild (Reinert 1991; Stahl 1981). In addition, adaptation to captivity can occur allowing those genotypes best suited for surviving and reproducing in captivity to increase in frequency, while those genotypes best suited for surviving and reproducing in the wild dwindle (Kohane and Parsons 1988; Allendorf 1993).

When appropriate behaviors are absent in captive-bred individuals, it may mean that those behaviors are learned. Learned behaviors, such as predator avoidance, probably depend on exposure to specific predators which may not occur in the natal ranges of translocated animals. However, the lack of a "hard-wired" genetic basis for these behaviors renders them no less critical with regard to successful reproduction and, ultimately, to fitness (see Bekoff 1989 for a discussion of behavioral development in carnivores).

Translocations may fail for many reasons, including non-inherited differences among populations, limits to phenotypic plasticity, and detrimental stochastic events. Several examples illustrate the problems inherent in translocating animals from one ecosystem to another.

Evans and Williamson (1976) described an attempted introduction of wild turkeys from an arid region of Texas to the wetter areas of eastern Texas. Although the dry-adapted birds survived, high humidity prevented them from nesting successfully, and the introduction failed.

Woodland caribou from two British Columbia (B.C.) populations (west-central and east-central) were transplanted into northern Idaho to augment a small remnant population (Warren 1990; Warren et al. 1996). Transplanted individuals had a tendency to retain the movement and feeding behavior of their original stocks. Caribou from west-central B.C. eat mainly terrestrial lichens in winter, whereas caribou from east-central B.C. eat arboreal lichens because the snow is too deep to dig through. After translocation, more east-central caribou emigrated from the transplant area, in keeping with the tendency of the parent population to emigrate more frequently than west-central caribou. Most west-central caribou died, and apparently starved while digging for lichens in winter, ignoring abundant arboreal lichens in the transplant area.

Lynx translocations have also proven to be problematic. Eighty-three lynx were translocated from the Yukon Territory into the Adirondack Mountains of New York in the late 1980s (Chapter 13). Nearly half the animals died within two years of being released and, in spite of considerable search effort, there is no recent evidence of lynx occurrence in the Adirondacks (K. Gustafson, personal communication). An ongoing lynx reintroduction effort involving the translocation of animals from Yukon and Alaska into Colorado has been fraught with problems, including the starvation of several individuals (Kloor 1999). Translocations are most likely to succeed between populations whose environments and ecological relationships are similar, especially with regard to climate, habitat, and community composition. We believe that translocation of closely related populations, with similar local adaptations, will have the highest probability of success. Furthermore, we believe that relocation from the core to the periphery of a species range will usually entail significant risk.

Outbreeding Depression

Interbreeding between two populations may result in a reduction in number, viability, or fitness of offspring, a phenomenon known as *outbreeding depression* (Templeton 1986; Waser and Price 1994). There are two mechanisms responsible for outbreeding depression: mixing of locally adapted populations, and disruption of *co-adapted gene complexes*, which are sets of genes that increase fitness when all are present in the individual (Templeton et al. 1986).

The first mechanism, interbreeding of animals from two locally adapted populations, produces offspring that may not be adapted to either location. There are several examples of translocation failures resulting from mixing locally adapted populations (Grieg 1979; Templeton 1986; Turcek 1951). Populations of the Tatra Mountain ibex in central Europe were supplemented with ibex from Turkey and the Sinai during the 1960s. The hybrids of these ibex rutted in early autumn instead of in winter (as the native ibex did), and the females gave birth in February in Czechoslovakia during the coldest time of the winter. The entire population went extinct because of the mixing of these groups (Grieg 1979).

A second mechanism that can cause outbreeding depression is the disruption of co-adapted gene complexes. The mixing of gene pools (e.g., by translocation of individuals with one set of co-adapted gene complexes to another population with a different set) can break down these gene complexes and cause a reduction in fitness (Dobzhansky 1948).

Natural Variation and Lynx Conservation

Resource managers have the complex task of applying the concepts discussed in this chapter within a legal context. The Endangered Species Act (ESA) will allow listing of “any subspecies of fish or wildlife or plants, and any distinct population segment of any species of vertebrate fish or wildlife which interbreeds when mature.” Only two subspecies of lynx have been described in North America: one in Newfoundland (*L.c. subsolanus*), and the other throughout the remainder of Canada, Alaska, and the contiguous United States (*L.c. canadensis*; Werdelin 1981). Thus, determining whether distinct population segments occur within this region is a critical conservation issue.

Evolutionarily Significant Units

The first U.S. management agency that comprehensively addressed the problem of defining distinct population segments was the National Marine Fisheries Service (NMFS). One of the missions of NMFS is to manage Pacific salmon, a species group with high levels of phenotypic variation (Allendorf et al. 1997). Waples (1991) proposed that a population be considered “distinct” if it represents an Evolutionarily Significant Unit (ESU) of the species (a term first coined by Ryder in 1986 with regard to prioritizing species for captive propagation efforts). To be considered an ESU, a population must be reproductively isolated from conspecific populations, and it must represent an important component of the evolutionary legacy of the species. According to Waples (1995) the evolutionary legacy of the species is “the genetic variability that is a product of past evolutionary events and that represents the reservoir upon which future evolutionary potential depends.”

When NMFS was asked to evaluate the status of spring-, summer-, and fall-run chinook salmon in the Snake River, they applied the ESU concept (USDC 1991; USDI and USDC 1996; Waples 1995). Large genetic differences separated fall from spring and summer fish, but it was unclear what the contribution of the Snake River fall-run chinook was to the “ecological-genetic diversity” of the species (Waples 1995). Water characteristics such as temperature and turbidity differ dramatically between the Snake River and the adjoining Columbia River, and it was believed that Snake River fall-run chinook had developed either physiological or behavioral adaptations to its river environment. These data, along with different oceanic distributions of the Columbia and Snake River fish, were used to classify Snake River fall-run chinook as an ESU. The spring and summer runs were distinct from the Columbia River chinook. However, the timing of the run (spring versus

summer) explained less than 10% of the genetic variation in the sample. Consequently, spring and summer runs were classified as one ESU.

In 1994, the U.S. Fish and Wildlife Service (USFWS) drafted a policy regarding the recognition of distinct vertebrate population segments under the ESA (USDI and USDC 1994). The goal was to use criteria similar to NMFS for defining a distinct population segment (i.e., an ESU). The USFWS proposed that distinct population segments would be defined according to the discreteness and significance of the population segment relative to the remainder of the species (USDI and USDC 1994, 1996). This policy has only recently been adopted (USDC 1996).

The ESU approach has been criticized from both biological and legal perspectives as being not biologically meaningful, too subjective, too specific to salmon, and relying too heavily on genetics (Rohlf 1994; Vogler and DeSalle 1994; see Waples 1995, 1998 for responses). A wide range of solutions have been proposed to address both the problem of subjectivity (see Moritz 1994) and reliance on DNA-based analyses (see Vogler and DeSalle 1994). All participants in this debate appear to agree that understanding observable variation in nature is critical to identifying distinct population segments for conservation.

Because we are often unable to tell if adaptive traits are inherited, an ESU policy that focuses only on inherited traits will fail to identify potentially important distinct population segments. We recommend that all aspects of the natural history of lynx be considered when evaluating potential ESUs for lynx. This includes not only data on neutral genetic markers (e.g., microsatellite DNA), but also potentially adaptive traits inferred from physiological, behavioral, morphological, and ecological studies.

Implications for Lynx Conservation

We know virtually nothing about levels of natural variation in lynx populations. However, we do know that the geographic range of lynx covers a broad range of environmental conditions, especially with regard to habitat structure, habitat ecology, and predator/prey communities (Chapter 14). Additionally, the environment at the core of the lynx range is very different ecologically from the environment at the southern periphery of the species range (Chapter 3). We also know, however, that individual lynx are capable of long-range movements, and that all populations are restricted to boreal forest habitats and appear to rely on snowshoe hares as prey.

Understanding the nature of variation among lynx populations and its implications for conservation will require studies of the genetic structure of subpopulations, estimates of historical and current gene flow between peripheral and core populations, and studies of comparative ecology

throughout the range of lynx. Until we understand the nature of geographic variation in lynx populations, it would seem prudent to assume the existence of important genetic and non-genetic differences among populations, especially those that are distant and/or relatively isolated.

Conclusions

In this review, we have attempted to show that (1) natural variation among populations is prevalent in nature, (2) conservation assessments and plans need to explicitly address patterns of natural variation among populations, whether it is inherited or not and (3) such assessments need to be concerned not only with genotypes, but also with the plasticity of those genotypes to produce different phenotypes. The preservation of natural variation will, in part, be concerned with the conservation of genetic diversity and genetic adaptations to local environments. Protection of this type of diversity is mandated by the ESA and can be addressed through the Evolutionarily Significant Unit (ESU) policy recently adopted by the Departments of Interior and Commerce. However, implementation of this policy should include explicit consideration of both inherited and non-inherited variation.

Some non-inherited traits that vary between populations are *ultimately* under genetic control. Traits such as phenotypic plasticity allow species to respond to changing environments and to potentially different environmental conditions found at the periphery of a species' range. Phenotypes which are products of specific environments become endangered if we lose or modify those environments. It would be naive to think that we could recreate an extinct phenotype by taking a similar genotype and subjecting it to comparable environmental conditions. Similarly, we may disrupt adaptive phenotypic responses by introducing individuals to the population that lack the genetic potential to make appropriate phenotypic adjustments. And finally, culturally inherited behaviors are likely to be especially important in higher vertebrates having complex behavioral patterns and socially or parentally facilitated behavioral development.

Traits that are genetically determined and those that are largely determined by the environment are part of a continuum and, in many cases, it may be impossible to distinguish between the two. Does it matter if differences are genetic, if such differences improve fitness and convey a selective advantage by improving reproductive success? The answer is a qualified "no." In the case of genetic adaptations, this advantage is more or less fixed over intermediate time periods (e.g., hundreds of years given a more or less stable environment), thus contributing to the long-term evolutionary potential of the species. In the case of non-genetic differences, the potential for

change over the short term may mediate survival rates leading to long-term change. For example, new behaviors learned in response to new environmental challenges could result in improved survival, allowing populations to persist and acclimate to changing conditions. In this scenario, if environments change quickly and dramatically, as is often the case when translocating animals, a lack of behavioral plasticity could lead to increased mortality rates and, eventually, local extirpation.

Similarly, management decisions made on the basis of observed habitat relationships in one population could result in detrimental effects on another population occupying a substantially different environment. For example, forest management practices determined to be beneficial to lynx in the taiga may not be appropriate in southern boreal forests of the western montane region, where ecological conditions are dramatically different. In other words, the translocation of scientific knowledge from one population to another can be as risky as the physical translocation of animals. In either case, the risk of undesirable results will increase with ecosystem dissimilarities and/or geographic distance.

Implications for Management

Because translocations and reintroductions are inherently risky even under optimal conditions, they should be used only when other management options have failed. Conservation objectives are more likely to be met by maintaining and/or enhancing habitat conditions for lynx to provide opportunities for them to recolonize former portions of their range. If deemed necessary, reintroductions into peripheral populations should be done with lynx from other peripheral populations, neighboring populations, or genetically similar populations. It is risky to use individuals from captive, distant, or ecologically dissimilar populations.

Neutral genetic markers can detect the structuring of populations and aid in the identification of source populations for translocated individuals. However, we caution that analyses of neutral markers cannot detect differences in adaptive traits between populations. Thus, even if no subdivision of populations is detected with such analyses, adaptive genetic differences may still exist between populations.

Lastly, it is critical to consider both inherited and non-inherited variation when manipulating lynx populations or managing their habitat. We recommend that managers assume the existence of important genetic and non-genetic differences between distant and/or relatively isolated lynx populations until proven otherwise.

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