Perspective

Bureaucratic Mischief: Recognizing Endangered Species and Subspecies

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THE U.S. ENDANGERED SPECIES ACT OF 1973 WAS designed to identify and protect plant and animal species whose number and habitat had become sufficiently depleted to critically threaten their survival. The Act as amended specifically affords protection to three categories of biological taxa: species, subspecies, and populations. The operational definition of these terms, inadequate taxonomy, and the periodic occurrence of hybridization between species and subspecies have led to confusion, conflict, and, we believe, certain misinterpretations of the Act by well-intentioned government officials.

The listing of certain species as endangered has encouraged an increase in investigation of these taxa, notably in molecular genetics and field ecology (*1*). In some cases the molecular genetic results contradicted previous ideas about species integrity or taxonomic distinctions that were based on phenotypic (morphological) descriptions. Unfortunately these traditional taxonomic designations have been and continue to be the bases for management and eligibility for protection. This is a significant problem because the Endangered Species Act not only protects listed taxa from hunting, habitat exploitation, and other perils associated with human coexistence, but also provides significant financial resources for the effort to protect these species and to stabilize their populations. To illustrate the problem we summarize the interpretive difficulties posed by molecular results for four endangered groups.

The Florida panther. This is a small population of mountain lion (also called cougar or puma) that descended from the *Felis concolor coryi* subspecies that ranged throughout the southern United States in the 19th century (*2*). The few remaining panthers (≤ 50) living in southern Florida show significant physiological and reproductive impairments that are likely the consequence of inbreeding depression. A recent allozyme and mitochondrial DNA (mtDNA) analysis of the population revealed that two very distinct genetic stocks were living in Florida (*2*), one that resembled other North American pumas and another that was more closely related to a puma subspecies that had evolved in South America. Apparently seven animals from a captive stock (that later turned out to be a mixture of authentic *F. concolor coryi* and South American founders) were released into the Everglades between 1957 and 1967 and promptly forgotten. Today the founder ecosystem contains a mixture of two subspecies.

The genetic advantages of introducing some additional genetic material into a population suffering from inbreeding would have been comforting except for one detail. Three opinions from the Solicitor's Office of the Department of the Interior (which is the counsel of the U.S. Fish and Wildlife Service) have ruled with the force of precedent that hybrids between endangered species, subspecies, or populations cannot be protected. Their opinions, referred to here as the Hybrid Policy, concluded that protection of hybrids would not serve to recover listed species and would likely jeopardize that species' continued existence. The current status of the Florida panther as endangered could be challenged or even revoked under a strict interpretation of the Hybrid Policy.

The gray wolf (*Canis lupus*). This wolf has suffered severe demographic contractions in North America owing to habitat depletion associated with the spread of agriculture. An mtDNA survey of wolves and coyotes across the northern United States (*5*) and Canada (*3*) revealed evidence for the presence of coyote mtDNA in wolf populations, but not vice versa, in a restricted region ranging from northern Minnesota to southern Quebec. Anecdotal accounts of wolf-coyote hybridization, the recent mtDNA results, and knowledge of the Hybrid Policy have prompted a formal petition from the Farm Bureaus of Wyoming, Montana, and Idaho to the U.S. Department of Interior that *C. lupus* be removed from Endangered and Threatened Lists. Similar logic has also been used to prevent reintroduction of gray wolves into Yellowstone National Park.

The red wolf (*Canis rufus*). The taxonomic status of the red wolf has been disputed for some time, with certain experts calling it a species and others suggesting that it be considered a subspecies of gray wolf (*4*). Extensive morphological studies plus recent molecular genetic analyses of captive red wolves and museum specimens (*3, 4*) raised the possibility that the red wolf group represented a hybrid between gray wolf subspecies and coyotes. Therefore, protection of the red wolf would be imperiled by strict enforcement of the Hybrid Policy.

The dusky seaside sparrow (*Ammodramus maritimus nigrescens*). This is a melanistic coastal subspecies that until recently inhabited the eastern coast of Florida (*5*). The population dropped until 1980, when five of these were brought into captivity and crossed with a morphologically similar subspecies from the gulf coast of Florida, Scott's seaside sparrow, *A. m. peninsulae*. The opinion of the Solicitor's Office in 1981 stated that the production of hybrids between the two subspecies (or any others) would not be in the interest of the Endangered Species Act. The dusky seaside sparrow became extinct in 1987.

These four examples emphasize the critical role that taxonomy plays in the enforcement of the Endangered Species Act, and the potential power of molecular genetic data in resolving taxonomic relationships and the unfavorable (and unnatural) consequences of the Hybrid Policy. To aid this process, we offer definitions for species and subspecies that can be applied to threatened fauna.

The Biological Species Concept. In 1940, Mayr (*6*) proposed the Biological Species Concept (BSC) that defined a species as "groups of actually or potentially interbreeding populations that are reproductively isolated from other such groups." Reproductive isolation, the primary component of the BSC, refers to the heritable tendency of distinct species to avoid gene flow or interbreeding even when they are brought into physical contact in nature. In clarifying this concept Mayr (*6*) noted that most species occupy distinct ecological niches and that this ecological distinctiveness is the keystone of evolution. Although various alternative species concepts and criticisms (*7, 8*) have appeared, the BSC has emerged as a biological paradigm with its major components affirmed (*8*).

A major strength of the BSC is that it reflects the occurrence in natural situations of the irreversible process of speciation. It emphasizes reproductive isolation as the sole discriminator of species as whole entities, but acknowledges the occasional production of hybrid individuals or even hybrid zones (*9, 10*). Further, the BSC acknowledges the existence of appreciable genetic diversity within species that is often partitioned geographically (or temporally) by population subdivision into subspecies, ordinarily under conditions of allopatry (reproductive barriers are geographic). The distinction however is that natural occurrences of hybrid individuals or hybrid

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zones between recognizable species do not disintegrate the genetic integrity of the species, while hybridizations between subspecies produce gene flow and genetic mixing. Reproductive isolation in nature provides an effective protective device against genetic disintegration of the species genotype (*6, 8*).

The subspecies category has been defined as "a geographically defined aggregate of local populations which differ taxonomically from other subdivisions of the species" (*6*). A valuable recent modification (*11*) urged that the evidence for BSC subspecies designation should come from the concordant distribution of multiple, independent, genetically based traits. In an attempt to provide formal criteria for subspecies classification we offer the following guidelines: Members of a subspecies share a unique geographic range or habitat, a group of phylogenetically concordant phenotypic characters, and a unique natural history relative to other subdivisions of the species. Because they are below the species level, different subspecies are reproductively compatible. They will normally be allopatric and they will exhibit recognizable phylogenetic partitioning, because of the time-dependent accumulation of genetic difference in the absence of gene flow. Most subspecies will be monophyletic, however they may also derive from ancestral subspecies hybridization (*12*).

In our view an allopatric subspecies has four possible fates; it may: (i) go extinct; (ii) exchange genes with another subspecies and become a new "mixed" subspecies; (iii) by genetic drift, selection, subdivision, or other demographic processes change its genetic character over time to become one or more new subspecies; and (iv) if effectively isolated, become a new species by acquiring genetic isolating mechanisms. It it not possible to know which subspecies will become new species, but they all have this potential. Moreover, as the time of allopatry increases, the probability of genetic differentiation increases, and included within these differentiative changes are ecologically relevant adaptations. The possibility that a subspecies carries such adaptations coupled with the potential to become a unique new species are compelling reasons for affording them protection against extinction.

The Hybrid Policy of the Endangered Species Act. The understanding of the BSC species, of subspecies, and of different categories of hybridization now leads to a recommendation for the Hybrid Policy with respect to endangered species. The Hybrid Policy that discourages production of hybrids between species seems appropriate and should be affirmed. The Hybrid Policy, however, should not imperil the listing or protection of species with sympatric hybrid zones as long as the existence of the zones does not disintegrate the genetic organization of the species in contact. Preclusion of protection for interspecies hybrids would correctly discourage capricious interbreeding between species in captivity as well as the facilitated introduction of species into natural habitats that are occupied by closely related but distinct species (*13*). For subspecies and threatened populations, the Hybrid Policy should be dropped. Subspecies can and do interbreed as a natural process whenever they are in contact; that is why they are not species. Subspecies that are defined by genealogical concordance and geographic partitioning can be protected because of their potential and their acquisition of unique characteristics; they represent important components of biological diversity. Occasional introgression or interbreeding should not be viewed as inconsistent with subspecies status; they simply change the phylogenetic description. Because subspecies do acquire ecological adaptations, the managed facilitation of subspecies mixing would generally be discouraged although, in certain extreme cases, it may be justified.

Under application of BSC principles a recommended easement of the Hybrid Policy leads to the following:

1) The Florida panther would receive continued protection since it clearly qualifies as a subspecies. In fact, the present population may be better off as a result of acquisition of new genes because of the multiple congenital difficulties that apparently emerged as a result of inbreeding in the ancestral *F. concolor coryi* (*2*).

2) The natural hybridization of gray wolf and coyote is limited to a narrow hybrid zone that developed recently in the Midwest. Since it does not affect the genetic integrity of either species elsewhere in their ranges, there is no justification for eliminating protection of the gray wolf species.

3) The status of red wolf is difficult because it is extinct in the wild and the captive bred survivors are likely descended from natural hybridization between coyotes and an extinct subspecies of gray wolves. The case for protection would be that the captive red wolves are the only available descendants of that historic subspecies (*13*).

4) The dusky seaside sparrow had a series of molecular characters that distinguished it from Gulf Coast subspecies but were indistinguishable from Atlantic Coast populations (*5*). Phylogenetic concordance provides justification for revising the taxonomy of the seaside sparrow complex to designate Gulf Coast and an Atlantic Coast subspecies (*2, 8*). Should either group become rare, protection under the Endangered Species Act could be contemplated.

There are many additional examples of confusion and misdirected judgments in the task of conserving endangered species (*1, 14*). It is important that legal opinions recognize the important distinction between species and subspecies. Biological species do not form hybrids that disintegrate population genetic organization, but subspecies may. The Hybrid Policy of the Endangered Species Act should discourage hybridization between species, but should not be applied to subspecies because the latter retain the potential to freely interbreed as part of ongoing natural processes.

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15. The authors are grateful to J. Avise, B. Grant, C. Stephens, R. Wayne, and U. Seal.