Got Hybridization? A Multidisciplinary Approach for Informing Science Policy

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Hybridization in the wild between closely related species is not unusual. In some cases, hybridization may prove beneficial for a rare taxon. Under certain conditions, however, a rare taxon can be driven rapidly to extinction by hybridizing with a more common taxon. This problem is urgent because human activities are increasingly bringing together cross-compatible species that were previously geographically isolated. US conservation policy has yet to address how to deal with hybrid-derived individuals whose ancestry includes an endangered species. Developing sound science–based conservation policy that addresses hybridization requires cross-disciplinary social-science and life-science research to address the following two questions: (1) How do human decisions with regard to species protection, trade, transportation, land use, and other factors affect the opportunities for, and rates of hybridization between, rare species and more common relatives? and (2) How do the positive or negative perceived values regarding hybrids and hybrid-derived individuals compare with values regarding their nonhybridized counterparts from social, cultural, economic, and environmental perspectives? In this article we explore the ways to inform such policy using a multidisciplinary approach.

Keywords: conservation, hybridization, extinction, anthropogenic change, policy

Evolution is ongoing. In many cases, the process of speciation is accompanied by the gradual evolution of reproductive isolation. Hence, reproductive barriers between closely related taxa are not always absolute, and as a result, closely related species of animals, plants, and even microorganisms may hybridize when they come into proximity in the wild (Arnold 2006). Hybrid progeny of some species may be weak or sterile. The sterility of the mule, a hybrid between horse and donkey, is the classic example of hybrid sterility. But hybrids between other taxa may be vigorous, persistent, and sometimes invasive. For example, Europe's notorious "weed beet" is a hybrid of the crop sugar beet and the wild sea beet (reviewed in Ellstrand 2003). In certain cases, hybrids and their descendants may form "hybrid swarms," multigenerational populations that in some cases occupy unique, often "hybrid" intermediate ecological habitats (Anderson 1949, Arnold 2006).

The reality of incomplete reproductive isolation presents a challenge for conservation policy. It is not unusual for endangered taxa to mate successfully with more common, cross-compatible wild relatives. Such hybridization raises interesting questions: Should animals that are morphologically and behaviorally identical to the endangered Great Lakes gray wolf be protected, should genetic analysis reveal that they have ancestors that were coyotes (Koblmüller et al. 2009)? The last of the highly inbred Florida panthers (*Felis concolor coryi*) were riddled with genetic defects, but was it wise to introduce another subspecies from Texas (*Felis concolor stanleyana*) to mate with them, even if that infusion of genetic variation boosted the fitness of their offspring (Pimm et al. 2006)? What steps should be taken to protect the last 11 adults of Catalina mountain mahogany, given that 5 of them are of recent hybrid ancestry (Rieseberg and Gerber 1995)? Should feral domesticated cats be allowed to mate with threatened European wildcats until the latter can no longer be distinguished from the domesticates (Lecis et al. 2006)?

Almost two decades ago, O'Brien and Mayr (1991) lamented what they named the "hybrid policy" of the US Fish and Wildlife Service (USFWS). The de facto policy of that agency was, they asserted, "that hybrids between endangered species, subspecies, or populations cannot be protected." O'Brien and Mayr argued that the strict interpretation of this policy could interfere with the protection of some endangered taxa. In particular, they pointed out that the policy would not protect individuals with *any* history of genetic admixture, even if the

BioScience 60: 384–388. ISSN 0006-3568, electronic ISSN 1525-3244. doi:10.1525/bio.2010.60.5.8

historical genetic contribution of a nonthreatened taxon was trivial, or if a limited genetic contribution of a nonthreatened taxon served to increase fitness in the face of inbreeding depression or a biological enemy. Following O'Brien and Mayr's (1991) recognition that hybrid ancestry could actually be beneficial for an endangered taxon, the concept of genetic rescue has received increasing attention (Tallmon et al. 2004, Pimm et al. 2006).

At the same time, there is growing recognition that in some circumstances spontaneous hybridization may pose severe conservation problems (Rhymer and Simberloff 1996, Levin 2002). For example, hybridization with the introduced mallard is the major conservation problem facing the endangered Hawaiian duck, and has led to its probable extirpation on the islands of Oahu and Hawaii (BirdLife International 2008). This problem is not restricted to animals: Some plant species are also threatened with extinction by hybridization (EBH; Levin et al. 1996). In fact, hybridization played a major role in the extinction in the wild of a relative of cultivated rice in Taiwan (Kiang et al 1979). Spontaneous hybridization with London plane tree (*Platanus* × *acerifolia*), a widely planted horticultural cultivar, has led to the erosion of species borders for at least three natural *Platanus* species (Whitlock 2003).

Theoretical studies have found that under certain realistic conditions EBH can be surprisingly rapid, sometimes occurring in only a few generations (Huxel 1999, Epifanio and Philipp 2000, Wolf et al. 2001, Ferdy and Austerlitz 2002). The resulting population might quickly evolve to appear to be simply a variant population of the common taxon. Such rapid morphological change may explain why there are many reports of a population previously "misidentified" as a rare taxon and subsequently "reidentified" as a common congener.

The many faces of hybridization in conservation had become apparent when Allendorf and colleagues (2001) revisited the problem about a decade after O'Brien and Mayr (1991). By that time, the hybrid policy had been withdrawn, and an "intercross policy" was proposed jointly by the USFWS and the National Marine Fisheries Service. To this day this policy has been neither approved nor rejected; as such, there is no official US policy to provide guidance for dealing with hybrids. In their review, Allendorf and colleagues (2001) pointed out that there are many types of hybridization—natural and anthropogenic—resulting in a variety of impacts, depending on the history, ecology, and genetics of the individuals involved. Allendorf and colleagues (2001) emphasized that under certain circumstances, extensive hybridization may end in the extinction of an endangered taxon, and they suggest any hybridization policy must be flexible enough to deal with cases where hybridization is beneficial to the taxon at risk and with cases when hybridization increases the risk of extinction. Haig and Allendorf (2006) reinforced this view in their review of the history of hybrid issues related to the US Endangered Species Act. They concluded that "establishing an effective policy regarding hybrids will not be simple given the variability of situations" (Haig and Allendorf 2006).

The situation has also proven challenging beyond the borders of the United States. Only one country, the Republic of South Africa, has endangered species legislation that mentions hybrids.

A need for interdisciplinary research

We agree with Allendorf and colleagues (2001) that part of the challenge is the biological variability of the types and consequences of hybridization. But another reason that a conservation policy regarding hybrids may be so difficult to establish is that the issues—like many in the field of conservation—are not simply those of life science; many lie at the interface of the life and social sciences. We suggest that joint social science–life science research is imperative to inform the development of a conservation policy regarding hybrids for two reasons.

First, human activities are increasing the opportunities for hybridization. It is recognized that human activity now plays the primary role in increasing the probability of EBH (Seehausen et al. 2008). At the local scale, human disturbance, whether purposeful (e.g., landscaping) or accidental, plays a role in the establishment and spread of exotic species that are cross-compatible with native congeners. Such disturbances can also create intermediate "hybridized" habitats that permit the spatial proximity of related species with different niches (Anderson 1949, Arnold 2006). At the landscape scale, urban and suburban populations are in increasingly frequent contact with wildlands.

Globally, human-influenced ecosystem alterations such as climate change are modifying the spatial distribution of some species (e.g., Parmesan and Yohe 2003). Global transport moves species intentionally and unintentionally between countries and continents. Intercontinental trade is well known for inadvertently introducing organisms, such as rats, lampreys, and zebra mussels, but we should not dismiss intentional anthropogenic dispersal. Economically important organisms, such as horticultural, food, and pet species, are often introduced into regions far from their places of origin. Many of these intentionally introduced exotics escape from their introduced locations and form free-living populations (e.g., Williams 1980, Gressel 2005). Expanded ranges—whether native or exotic—may bring previously isolated relatives into contact. Such close contact results in new or greater opportunities for interspecific hybridization (figure 1). Dozens, perhaps hundreds, of exotic plant cultivars commercially available in North America, including trees (e.g., pine, willow, oak), shrubs (e.g., rose, azalea), and herbs (e.g., columbine, larkspur, lily), are capable of hybridizing with rare native taxa. In fact, such plants are typically preselected for their ability to hybridize. They often have been bred for drought tolerance, the ability to produce large numbers of flowers, or as pollinator attractants; these are the sorts of traits that may act to accelerate the pace of introgression of exotic alleles into native populations.

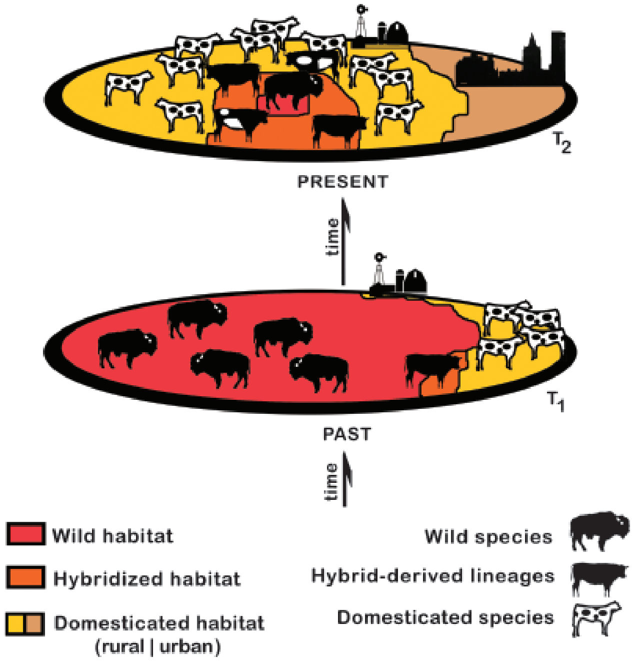

Figure 1. Human activities often enhance opportunities for the creation and persistence of hybrids by bringing previously isolated relatives into contact and creating intermediate habitats suitable for hybrids and their descendants. Our example involves hybridization and introgression of domestic cattle alleles into bison populations, a conservation issue that has already received considerable attention (Halbert and Derr 2007, Vogel et al. 2007).

From the life-science perspective, the specific details and relative importance of such anthropogenic factors in EBH are poorly understood. What are the relative roles of dispersal through human-mediated transport, anthropogenic disturbance, ecosystem conversion, and climate change in bringing together previously isolated cross-compatible species? What is the relative role of intentional versus unintentional anthropogenic introduction in cases where hybridization puts an endangered taxon at further risk? How important are multiple introductions versus a single introduction? Should the decision to introduce an exotic species involve assessing the potential for hybridization with an at-risk species in the region of introduction?

On the social-science end, even less is known about how human decisions affect these processes. Consider the specific example of international trade. The intentional transport of plants intended for ornamental sale (Reichard and White 2001) involves decisions about which species to choose, how many individuals to transport, the means of transportation, the locations of the source and delivery, and the details of retail or wholesale dissemination. These decisions are determined largely by economic, cultural, legal, and political factors, with little or no consideration given to the probability of the introduced species having an impact on native organisms and habitats. Clearly, answering the question, "How do human decisions with regard to ornamental plant trade affect the opportunities for and rates of hybridization between exotic species and native relatives that are rare or endangered?" would be easier with the help of economic, political science, anthropological, and legal expertise contributed by social scientists, in addition to botanical, genetic, and conservation expertise from the life sciences.

Second, individually and collectively, humans have developed their own value-laden perceptions about endangered species and hybridization. While virtually all current threats to native species have anthropogenic origins, hybridization may be perceived by the public as a more esoteric threat than, say, poaching, because the former is less obvious. Hybridization may even be considered intrinsically beneficial (think hybrid vigor) or intrinsically scary (think miscegenation). Compounding the issue, the actual consequences of hybridization or subsequent introgression to endangered taxa are idiosyncratic: They are sometimes beneficial to an endangered taxon, sometimes detrimental, and sometimes insignificant (e.g., Ellstrand and Elam 1993, Allendorf et al. 2001, Arnold 2006).

Therefore, before we design a hybrid conservation policy, we need more information about the relative value of hybrids, whether from biological and environmental perspectives or from social, cultural, or economic points of view. The latter values are of particular importance because stakeholders' perception of species at risk may be critical to their support of conservation initiatives and the subsequent enforcement of legislation or implementation of management plans. The establishment of habitat conservation plans in recent years has made it necessary to include a growing number of local stakeholders in conservation initiatives. Social-science research can be used to better identify appropriate stakeholders who represent the spectrum of interests. This multiple-perspective approach has the potential to yield more realistic conservation plans for the species and habitats under consideration (Melious and Thornton 1999).

EBH presents what may appear to be a unique paradox, but the issues it raises in fact epitomize common difficulties and misperceptions about conservation. Conservation supporters and opponents, along with many in the scientific community, tend to conceptualize the natural environment and its protection in discrete units (e.g., landscapes, species, subspecies). The messy reality of the world is that all of these units—except perhaps some species (Rieseberg et al. 2006)—are often inconveniently less discrete than policymakers would like. Species are often not fully reproductively isolated from other species (Arnold 2006), and subspecies—which are often protected—are by definition never reproductively isolated from other conspecific subspecies. Likewise, ecosystems and landscapes are not neatly contained in space or time; indeed, wilderness is neither pristine nor clearly bounded (e.g., Botkin 1990, Gómez-Pompa and Kaus 1992, Cronon 1998).

Stakeholders in a given region will vary in their approaches to incorporating hybrids into endangered species conservation. Their approaches are likely to include both natural science and social science components. Thus, conservation decisionmaking must be informed by biological information as well as culturally and economically based perceptions regarding the value of a species' unique integrity or of a hybrid's form—issues raised by the value-laden questions we presented in the introduction of this article. The values and trade-offs of hybridization are not straightforward. Deliberate hybridization by plant breeders between domesticated and wild taxa is positively valued as part of the evolutionary processes of plant and animal domestication and improvement. A classic example is the tomato, whose cultivars hold as many as six different disease-resistant genes that were introgressed from wild relatives (Rick 1995). But spontaneous hybridization within already-domesticated populations can also be negatively valued, such as in the case of the Africanized bee. How can such differing values be incorporated into practical conservation policy?

The research necessary to inform the development of a conservation policy that includes hybrids lies at the interface between life science and social science. While all conservation issues have social relevance, the values associated with EBH can be more nuanced and harder to extract than those commonly considered in conservation policy. For example, in critical habitat designations, decisions about which species to protect require evaluation of the trade-offs between economic losses and species declines. Arnold (2004) pointed to "the involvement of natural hybridization, in its broadest sense, in the formation of some of humankind's best assets and worst banes." Yet the conservation ethic often values "being wild" at the landscape to genetic level, meaning, in the case of species, not hybridized. Without entering the discussion of wildness and wilderness as human constructs in their own rights, conservation models built on the supposed purity of wild species are difficult to negotiate, implement, or enforce when genetic introgression into endangered populations becomes an ongoing occurrence rather than an exception to the rule. Clearly, if a rare taxon experiences repeated and extensive gene flow from a common taxon, it will eventually evolve into the common one. At the same time, we should not relegate all entities with any degree of hybridization in their ancestry to the trash heap of extinction. Carefully managed, limited introgression from a more common taxon may be the only way to genetically rescue one that is endangered (Tallmon et al. 2004, Pimm et al. 2006).

In a sense, EBH shines a light on the broader, long-standing conservation issues (NRC 1995) of "What, precisely, should be saved?" and "Should every human-defined taxon be saved at all costs?" In the narrower context of EBH, these questions raise the important philosophical and cultural issue of whether a hybridized taxon should be considered the same as one of its prehybridized parental taxa. A social-science research contribution is necessary to understand why different people reach different conclusions regarding the composition and organization of the natural world. When it comes to the question, "What actions should be taken with regard to hybrids and hybrid-derived individuals compared with their nonhybridized counterparts?" life science may be able to provide the data on numbers of individuals, their genetics, their reproductive isolation, and, through modeling, the genetic outcomes of different management strategies. However, data and theory from the social sciences of anthropology, economics, sociology, and environmental ethics are necessary to estimate the social costs and benefits of those strategies, as well as their likelihood of adoption and ultimate success.

Conclusions

A reasonable conservation policy that addresses hybrids must consider how human actions increase opportunities for hybridization and the spectrum of values that society places on different kinds of hybrids. Underpinned by these considerations, policy can propose appropriate management action. We urge life scientists and social scientists to join together to address how the coupling of human activities and species biology has consequences for our planet's endangered biota in the context of societal values. This approach necessitates a genuine synthesis across multiple disciplines such as environmental ethics, history, political science, economics, geography, anthropology, genetics, ecology, systematics, and evolutionary biology. Cross-disciplinary endeavors present unique challenges, however the results emerging from such an integrated research program would go a long way toward the development of a flexible and sound conservation policy regarding hybrids.

Acknowledgments

This work was supported by funding from National Science Foundation Biocomplexity Grant (DEB-0409984 to NCE). We thank Diane Elam, Janet Leak-Garcia, Joanne Heraty, and Sylvia Heredia for their insights and comments on an earlier draft of this manuscript.

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