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Perspective

Perspectives on the conservation of wild hybrids

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ABSTRACT

Hybridization processes are widespread throughout the taxonomic range and require conservation recognition. Science can help us understand hybridization processes but not whether and when we ought to conserve hybrids. Important questions include the role of humans in hybridization and the value we place on natural and human-induced hybrids concerning their ecological function. Certain hybrids resulting from human actions have replaced the ecological role of extirpated or extinct parent taxa and this ecological role should be preserved. Conservation policies must increasingly recognize populations of wild organisms that hybridize naturally within the context of their historical ecological role. Natural selection acts on individual organisms and the range of characteristics displayed by individual hybrids constitute raw material for evolution. Guidelines must consider the conservation value of individuals and the ethical aspects of removing hybrids for the purpose of conserving population genetic integrity. Conservation policies should focus on protecting the ecological role of taxa affected by hybridization. An informative example is North American canids (*Canis*), where body size, prey availability, and human landscape modifications may interact and impose local selective pressures. Gray wolves (*Canis lupus*) and eastern wolves (*Canis lycaon* or *Canis lupus lycaon*) or Great Lakes wolves appear to hybridize naturally within the context of their historical ecological role. In contrast, eastern coyotes (*C. latrans*) exhibit wolf ancestry and have partly replaced the ecological role of an extirpated parent taxa in parts of northeastern North America. The need for advancing conservation policies that reflect our current understanding of ecology and evolution is urgent.

Contents

1. Introduction

Hybridization, here defined as ‘interbreeding of individuals from genetically distinct populations, regardless of their taxonomic status’ (Rhymer and Simberloff, 1996), represents a complex and problematic topic. In part, this is because the term ‘hybrid’ has negative connotations and the extent of hybridization in wild organism (perhaps with the exception of plants) has until recently been underestimated (Rhymer and Simberloff, 1996; Allendorf et al., 2001; Mallet, 2005; Abbott et al., 2013). Science can help us understand hybridization processes but if and when we ought to conserve hybrid organisms is not, in itself, a scientific question.

Negative perceptions associated with the term hybrid are likely to influence the extent to which people value wild organisms of hybrid origin. Furthermore, many questions surround the conservation management of wild hybrids. Important issues include the

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role of human-caused environmental change in hybridization and the value we place on natural and human-induced hybrid organisms concerning their ecological function. Hybrid designations have been used to argue against conservation measures offered by endangered species legislation because hybrids have been ineligible from habitat and hunting protection (O'Brien, 1994). Hybrids may also be ignored because their presence can confound conservation efforts (e.g. Giese, 2005). Recent recognition of the historical importance of hybridization as a creative force in evolution is changing this view (Rhymer and Simberloff, 1996; Allendorf et al., 2001; Abbott et al., 2013). New findings suggest that hybridization is widespread throughout the taxonomic range and thus requires explicit recognition in conservation planning (Mallet, 2005).

Delineating species when they must, at the same time, be treated as evolutionary entities that are constantly adapting to their environment is inherently difficult (Hey et al., 2003; Isaac et al., 2004) and species taxa are increasingly recognized as an emerging property of population-level processes (Hart, 2011). Speciation processes are one of the least understood major features of evolution (Schluter, 2001) and new species taxa can be considered hypotheses that might be supported with new data or require future revision (Hey et al., 2003). Whereas certain sources of taxonomic uncertainty cannot easily be resolved, they must neither be ignored nor feared (Hey et al., 2003) and species resulting from historical hybridization (natural genetic admixture) should be eligible for protection like any other species (Allendorf et al., 2001). The conditions that represent endangerment and thus the need for protection are a normative determination; i.e., based on how humans choose to define this particular category. The extent to which these conditions are fulfilled is subsequently informed by scientific facts (Vucetich et al., 2006). To develop improved guidelines for the conservation of wild hybrids we must therefore first decide what it is we aim to conserve.

2. The ecological role of hybrids in altered environments

Conservation programs should aim to conserve dynamic processes such as evolution, which affect individuals and organisms, rather than trying to retain static features and behaviors (Templeton, 1994) including any particular type of morphology. Furthermore, Pimm (1991) has argued that long-term population ecology should be considered community ecology and he urges a shift from the idea of a 'balanced nature' toward a focus on understanding factors such as ecological resilience and resistance. Accordingly, it may be helpful to establish conservation priorities for hybrids that emphasize (1) the extent to which the hybrids in question are natural as opposed to the (likely) result of human activity and (2) their current ecological role in the local environment.

Wild hybrids often produce a mosaic of phenotypes, which might provide the opportunity for rapid adaptive radiation (Seehausen, 2004; Abbott et al., 2013). Hybridization processes therefore influence the ability to maintain native populations, their variation (Soulé, 1985), and function (Luck et al., 2003). Templeton's (1989) cohesion species concept suggests that a group of organisms can share genetic drift and adaptations through the processes of genetic exchange and ecological equivalence (Hey et al., 2003). Increasing environmental homogenization likely relaxes divergent selection (Seehausen et al., 2008). Human landscape change might therefore create a feedback-loop between gene flow and shared ecological niche, whereby increasing gene flow augments niche overlap and vice versa. Importantly, hybrid swarms can form even if there is selection against hybrids, as all their progeny will also be hybrids (Allendorf et al., 2001). Another factor to consider is that hybrid populations may be all that is left to fill a given ecological niche in a certain region. When setting hybrid conservation policies, considering the processes that caused hybridization and the processes these organisms are now participating in is necessary. The hybrids (or hybrid swarm) may have particular adaptations that permit them to succeed in their environment and these could be lost or reduced with any attempt at purging the gene pool.

Humans can influence directional selection on natural variation in size, shape, and behavior (e.g. Smith et al., 1995). Wild organisms are also increasingly adapting to human-modified landscapes in the form of hybridization (Seehausen et al., 2008; Song et al., 2011). Such human influence has implications for endangered species legislation, protected areas management, and efforts toward preserving evolutionary potential and connecting ecological processes across larger landscapes. Determining if hybridization is caused by natural or human factors is important but often difficult (Allendorf et al., 2001). Hybridization may have been influenced by both these processes, which can make it difficult to assign a conservation value for the resulting individuals and populations that accurately reflect their ecological and evolutionary roles. Additional complications are at times presented by the introgression of domestic or farmed species (e.g. Fraser et al., 2010; Scandura et al., 2011), which could introduce genes important for adaptation and genes that negatively affect survival in the wild.

With pervasive human changes to natural landscapes and trophic cascades (Estes et al., 2011), the ecological role of organisms such as invasive aliens (Schlaepper et al., 2011) and hybrids (Randi, 2010) require further attention in conservation policy and in setting priorities for nature conservation. One of the normative foundations of conservation biology is that evolution and biodiversity, and the maintenance of evolutionary potential, is good because of its inherent and instrumental value, and because humans generally enjoy variety (Soulé, 1985). Intensely human-managed and modified landscapes raise key questions about adaptation to human-dominated environments (Allendorf et al., 2001; Ashley et al., 2003; Despommier et al., 2007) as rapid evolution toward coexistence with humans can at times be the only option remaining to avoid extinction (Ashley et al., 2003).

The ethical conservation issues with respect to forcing wild organisms to adapt to altered environments are thus important to consider. Hybridization may play a positive role in permitting adaptation to and increased chances for survival in human-dominated landscapes (Mallet, 2005; Kyle et al., 2006). Hybridization might therefore be considered genetic pollution or, at times, genetic rescue.

3. Considerations for determining the conservation status of hybrids

Making conservation decisions and setting priorities for preservation despite incomplete knowledge is often necessary (Soulé, 1985). Complex issues include whether humans must manage the natural world (Bekoff and Jamieson, 1996) and the conservation value and role of invasive alien species (Schlaepper et al., 2011). Furthermore, conservation efforts often require balancing competing human values such as human liberty and social justice, which may at times be in direct conflict with conservation (Vucetich and Nelson, 2013). While we investigate hybridization, we ought to consider better efforts at protecting the ecological role of wild hybrids, including their possibility for dispersal and evolution via gene flow with naturally selected surrounding populations. This is the best means of preserving vulnerable populations at range margins where selection holds special importance (Bridle and Vines, 2006). Accordingly, the importance of individual organisms, including hybrids, needs further emphasis in conservation policy. Natural selection acts on individuals, and hybrid individuals represent raw material for selection that may alter the evolutionary trajectories of parent taxa or emerge as new evolutionary significant units (Crandall et al., 2000; Placyk et al., 2012). This may permit adaptive radiation of new forms well-suited to altered environments (e.g. Lamont et al., 2003; Fitzpatrick et al., 2010; Eroukhmanoff et al., 2013).

For many range-edge populations, human actions and conservation policies will influence the relative importance of natural and human-induced selection on hybrid individuals. If and where human-induced hybridization results in the call for removal (i.e. killing) of hybrids, the costs and benefits should be carefully evaluated from an ethical perspective that considers individual animals and populations (Vucetich and Nelson, 2007). Ethical norms are an inherent part of conservation biology (Soulé, 1985) and while these represent a collection of ideas, they also serve as guiding principles for human behavior (Jickling and Paquet, 2005; Vucetich and Nelson, 2013). Ethical concerns are receiving increasing attention and some scholars argue that human supremacy comes with undeniable ethical responsibilities for our treatment of non-human animals (Fox and Bekoff, 2009). When assessing the potential value of an admixed population, Allendorf et al. (2001) suggest considering the following factors: (1) Where few pure populations remain, hybridized populations have greater conservation and restoration value and (2) Where hybridized populations represent an important threat to the remaining pure population(s), the hybridized population have lower value.

Humanity's perhaps most pervasive influence on our environment is the loss of apex predators (Estes et al., 2011). In areas where we can still act to preserve ecological processes such as large predator–prey relationships, we ought to consider whether extinction by hybridization (Rhymer and Simberloff, 1996) is more defensible than extinction through other means such as unsustainable killing. Furthermore, we must reflect on whether widespread human-induced contemporary evolution (Ashley et al., 2003; Seehausen et al., 2008) is ethically acceptable and avoidable. Although humans will hold a dominant role for the foreseeable future (Soulé, 1985), explicitly considering these factors when shaping conservation policy remains important. We suggest the following conservation approach for wild hybrids:

(1) Where the landscape still supports parent taxa and their ecological role is susceptible to human-induced environmental change, priority should be on conserving the ecological and evolutionary processes that maintain naturally selected biodiversity.
(2) Where hybrids have filled the ecological niche (or parts thereof) of one or more parent taxa extirpated because of human activity, the focus should be on preserving the ecological role currently held by hybrids. This will subsequently help preserve the community structure of which the parent taxa were part, also in the event of a future natural restoration or reintroduction.

Below we discuss various considerations in hybrid conservation using as an illustration a genus for which there has been considerable research and much recent debate about taxonomy, conservation merit, and ecological importance.

4. Natural versus human-induced hybridization: an example and recommendations using the genus *Canis*

An informative conservation example is provided by hybridization in canids (*Canis*) of east central North America. These are believed to be affected by at least two hybridization events; one before European settlement and another during the past century (Wheeldon and White, 2009; vonHoldt et al., 2011). Coyotes (*C. latrans*) were historically present in eastern North America during parts of the Pleistocene more than 10,000 years before present (Nowak, 2003). The distribution and abundance of coyotes before European settlement is not known, although they were generally considered a species of the western prairie grasslands (Gier, 1975). Subsequent agricultural development is believed to have permitted extensive range expansion and rapid population growth (Gier, 1975; Lehman et al., 1991). Other canids implicated in hybridization include eastern wolves (*Canis lycaon* (Wilson et al., 2000) or *Canis lupus lycaon*) or Great Lakes wolves (Leonard and Wayne, 2008; Koblmüller et al., 2009) and gray wolves *C. lupus* (e.g. Wilson et al., 2009; Fain et al., 2010; Wheeldon et al., 2010). We hereafter refer to wolf-like North American canids with coyote-like mitochondrial DNA (mtDNA) haplotypes as eastern wolves (not including the reintroduced population of red wolves *C. rufus* in the southeastern US, which is also implicated in hybridization (Bohling and Waits, 2011)). We refer to the generally smaller and more coyote-like eastern North American canids with coyote or coyote-like mtDNA haplotypes as eastern coyotes. Eastern coyotes are generally larger and heavier than their western relatives but smaller than wolves, and there appears to be a gradient of intermediate canids with respect to phenotype and ecological role (Sears et al., 2003; Benson et al., 2012).

Recent studies report canid admixture from Virginia in the eastern US (Bozarth et al., 2011) to Saskatchewan in western Canada (Stronen et al., 2012). A hybrid swarm (Rhymer and Simberloff, 1996) of canids appears to have replaced wolves and parts of their ecological function in much of the northeastern United States (Kays et al., 2010). This hybrid swarm also shows introgression from domestic dogs *C. lupus familiaris* (vonHoldt et al., 2011; Monzón, 2012). Answers to the discussions surrounding the origin and classification of North American canids will likely depend on new findings in genetics and ecology, as well as the species boundaries (Randi, 2010; Hart, 2011; Hausdorf, 2011) and taxonomic designations (Cronin and Mech, 2009) applied. Despite the ongoing debate, considering the conservation policies guiding the management of these and other admixed populations is important. Canids occupy ecological niches at the top of the food chain. Their conservation will require preservation of ecological and evolutionary processes at a wider scale. Recent advances in genomics are permitting rapid progress in resolving hybrid ancestry and in evaluating the adaptive value of alternate genes in different environments (e.g. Monzón, 2012). However, even if we possessed perfect knowledge of the evolutionary history of organisms such as North American canids, the questions surrounding the ecological value of hybrids require an approach to science that acknowledges human values.

For eastern and gray wolves and their hybrids, we interpret genetic and ecological data (Villemure, 2003; Wheeldon and White, 2009; Loveless, 2010; Fain et al., 2010; vonHoldt et al., 2011, and others) to indicate that conservation policy should consider these canids as a complex of populations that naturally exchange genes, rather than two isolated evolutionary lineages (Allendorf et al., 2001). Further research may elucidate a more precise taxonomic or ecotype status for this wolf population with mixed ancestry (Cronin and Mech, 2009). Recent wolf-coyote hybridization seems to have been uncommon in the western Great Lakes region (Fain et al., 2010; Wheeldon et al., 2010, but see Koblmüller et al., 2009 for a different view). Furthermore, Schwartz and Vucetich (2009) question whether the threat to the integrity of the Great Lakes wolf from coyote introgression noted by Koblmüller et al. (2009) affects viability of ecosystem health and, if not, whether we ought to be concerned about genetic integrity. Eastern wolf-coyote hybridization, and the possibility of eastern wolves acting as a bridge for gene flow between gray wolves and coyotes

(Nowak, 2009; Wilson et al., 2009; Rutledge et al., 2010), represents a threat if it affects the ecological function of large ungulate predators. Whereas divergent mtDNA haplotypes indicate that gray and eastern wolves are not genetically exchangeable, they appear, at least in part, to be ecologically exchangeable (Templeton, 1989) as eastern wolves also prey on large ungulates (Loveless, 2010), although their influence on large ungulate population numbers may be less well studied to date. Accordingly, eastern wolves can be considered as an evolutionary significant unit (Crandall et al., 2000) that require protection against habitat loss, human harvest, and hybridization with coyotes (COSEWIC, 2001). Recent landscape genetic analyses also indicate that these elements may have synergistic effects (Benson et al., 2012).

Coyotes and wolves may have hybridized without human intervention before the arrival of European immigrants (vonHoldt et al., 2011), whereas current admixture appears to be human-induced (Lehman et al., 1991). Consequently, the extent to which coyote-wolf hybrids are considered natural and worthy of preservation is complex and may vary among regions. Notwithstanding, if eastern and gray wolves interbreed naturally within the context of their ecological role as predators of large ungulates, their hybrids should not be given lower conservation priority. They ought instead to be afforded increased attention because the ecological processes of which they are part are highly vulnerable to human actions and perceptions. Although current policies fail to provide adequate protection, we must avoid attempts to fit hybrids into the existing designations that permit or facilitate conservation actions and instead focus on revising policies to reflect advances in biological knowledge.

Characters that limit adaptability in one portion of a hybrid zone can also confer benefits to individuals at another portion (Good et al., 2000). In some areas large body size can be beneficial, whereas such individuals might be selected against in neighboring but different environments. In canids, this could result in a range of phenotypes in adjacent areas well within dispersal distance (Schmitz and Lavigne, 1987; Sears et al., 2003; Benson et al., 2012). In western North American wolves, large male body size appears to play an important role in subduing large ungulates, although smaller and faster females appear better at chasing down fleet-footed prey (MacNulty et al., 2009). These physical factors could influence the extent to which selection will act to preserve large male canids in human-modified landscapes, as replacement of large prey species with moderate size-prey (Lehman et al., 1991; Sears et al., 2003) could exacerbate the effects of landscape development and fragmentation.

The presence of large ungulates may be important for maintenance of the ecological role held by wolves. Immigration of large male wolves into southern range edge populations may help preserve the ecological function of large predators in areas with abundant or expanding coyote populations such as Mauricie National Park in southern Québec, Canada (Villemure, 2003) and Riding Mountain National Park in southern Manitoba, Canada (Carbyn, 1980). The presence of large ungulates also assures sympatry of gray wolves and coyotes by reducing potential for competitive exclusion of coyotes, which coexist with wolves as secondary feeders (Paquet, 1992). Whereas large males are successful in areas with abundant large ungulates that are difficult for coyotes to kill, they might be redundant in areas where large ungulates are progressively being replaced by smaller and faster species that demand alternate predatory skills. Hybrid canids preying primarily on mid-size prey (Sears et al., 2003) could become superior competitors in developed landscapes due to higher reproductive success (Arnold and Hodges, 1995; Good et al., 2000). This might extend into adjoining protected areas if hybrids have higher fitness than parental taxa and swamp local populations (Arnold and Hodges, 1995; Bridle and Vines, 2006). Eastern-gray wolf hybrids are known to occur in Canada from Saskatchewan to northeastern Québec and across the Great Lakes states in the US (Chambers et al., 2012; Stronen et al., 2012) but have no conservation status. Field observations indicate morphological, behavioral, and ecological characteristics consistent with those commonly known in wolves (Villemure, 2003; Nowak, 2009; Mech, 2011 and references therein), for which selective pressures associated with large ungulate prey species may be paramount. If these canids were to be deemed hybrids unworthy of protection, it could have negative consequences for the long-term conservation of local ecosystem processes (Estes et al., 2011).

Conversely, predation by long-distance pursuing predators may influence the continued viability of large ungulate populations. Human-modified ecotones are increasingly associated with infectious disease (Despommier et al., 2007) and infectious diseases in ungulates have major human health and economic implications (Simonetti, 1995). These diseases include bovine tuberculosis (*Mycobacterium bovis*) in Canada (Nishi et al., 2006), and brucellosis (*Brucella abortus*) and Chronic Wasting Disease (CWD) in the US and Canada (Thorne and Herriges, 1992; Williams and Miller, 2002; Wild et al., 2011). Disease can predispose ungulates to wolf predation (Williams and Miller, 2002; Krumm et al., 2005) and the two could interact in affecting large ungulate abundance (Joly and Messier, 2004). Wolf predation could remove CWD-infected deer from a population more effectively than human harvest, as the latter is more likely to be random in respect to presence of disease (Krumm et al., 2005; Wild et al., 2011). Furthermore, range edge wolf populations, including those occupying protected areas, are vulnerable to human-induced mortality and disruption of social structure (Villemure, 2003; Rutledge et al., 2009). Although co-evolution between ungulates and their pursuing predator may only date to the Pleistocene (Janis and Wilhelm, 1993), predation has played a major role in shaping modern ungulates (Dawkins and Krebs, 1979).

The scale of many predator–prey relationships does not easily allow experimental manipulation and the role of a pursuing predator is difficult to elucidate in regions that have not experienced its extended absence. Long-term research nonetheless indicates that predators have more profound consequences on ecosystem function than previously understood (Estes et al., 2011). Future research will improve our knowledge of hybridization in canids and other wild organisms. Yet, whether wolf-like canids with coyote-like mtDNA haplotypes are known as eastern wolves or Great Lakes wolves, and given species, subspecies or ecotype status, long-term conservation strategies for maintaining their ecological function will likely be similar.

For wild organisms in human-modified environments, adapting to altered conditions may augment the chance of survival (Smith et al., 1995). In certain developed areas of eastern North America, wolf-like forms appear to have persisted through hybridization with coyotes (Kyle et al., 2006; Wilson et al., 2009), whereas in the west wolves have simply disappeared from much of the human-dominated landscape, leaving only coyotes. Eastern coyotes are well adapted to living near humans and may play an increasing and influential ecosystem role in limiting mesocarnivores and preying on white-tailed deer (Gompper, 2002; Monzón, 2012), thus contributing to conservation of biodiversity and community structure. Eastern coyotes are nonetheless unlikely to be effective predators of moose and have therefore not filled the entire niche left by wolves.

The presence of pre-zygotic reproductive barriers in closely related taxa may be influenced by their history of sympatry (Crispo et al., 2011) and the historical range overlap of canids implicated in hybridization is uncertain, possibly fluctuating over time (Nowak, 2009). The evolutionary flexibility (or 'evolution-through-hybridization-ability') of eastern wolves may nonetheless allow adaptation to modified landscapes more readily than that of North American gray wolves. Wilson et al. (2000) suggest red and eastern wolves should be treated as one species, in which case the priorities for the red wolf recovery program might be reconsidered (Kyle et al., 2006). However, the southeastern US climate might have resulted in local adaptations and a possible example is reports of red wolf tolerance to heartworm (*Dirofilaria immitis*), a roundworm parasite transmitted through mosquitoes (Kelly et al., 2004). Such infections may occur in the US and in warmer regions of Canada (Kelly et al., 2004), although selective pressures to promote tolerance would likely be higher in the southeastern region currently occupied by the red wolf population.

For wild canid hybrids, we suggest the following conservation approach:

(1) Where canid hybrids continue to interact with historical prey species and habitats, natural selection will likely favor the persistence of wolf-like forms. Hence, priority should be on conserving ecological and evolutionary processes in the form of predator–prey relationships that maintain naturally selected biodiversity.
(2) Where hybrids have filled the ecological niche (or parts thereof) of one or more extirpated parent taxa, such as the eastern coyote in the northeastern United States and parts of southeastern Canada, the focus should be on preserving the ecological role currently held by these hybrids. This approach would subsequently help preserve the community structure of which the parent taxa were part; also in the event of a future natural restoration or reintroduction. Included in this category may be eastern coyotes that have historic traces of dog ancestry but are nonetheless fully integrated in wild populations.

5. Conclusion

Science can contribute much toward understanding the wild organisms and landscapes we wish to preserve. Science, however, cannot show us *what* it is that we wish to preserve. Increased attention is needed to establish conservation goals for entities such as hybrids that represent evolution-in-progress and to reflect on the role humans play as an evolutionary force shaping the wild organisms around us. We need to establish guidelines that explicitly incorporate conservation values for management of natural and human-induced hybridization. More information is needed to better understand hybridization dynamics and will no doubt be forthcoming. However, enough reliable knowledge exists to start improving conservation policy aimed at protecting the ecological role of hybrid organisms. There is an urgent need for advancing conservation policies that reflect our current understanding of ecology and evolution. Such policies must consider existing hybrids and their present ecological function.

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