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Source: Wildlife Biology, 2(3) : 143-150

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/wlb.1996.012

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Hybridization between native and introduced wildlife species: importance for conservation

Daniel Simberloff

Simberloff, D. 1996: Hybridization between native and introduced wildlife species: importance for conservation. - Wildl. Biol. 2: 143-150.

Molecular techniques show that hybridization can be a major conservation problem. Introgression can lessen genotypic variety and break up gene complexes coadapted to local environments. Gamete wastage can be a problem for hybridizing species even when gene flow does not occur. Birds and mammals introduced for game purposes have hybridized with native populations, a process often facilitated by habitat modification. Further, translocation and stock enhancement programs can lead to loss of well-adapted genotypes. These problems increase as populations become fragmented and isolated, because finding mates is harder and habitat differences that bar reproduction are obliterated. What to do about hybridization is sometimes not obvious. Even if the problem is seen as important, often little can be done. Culling may be impossible because of difficulties in recognizing introgressed individuals. Wildlife biologists and managers should work to prevent introductions and translocations if hybridization problems cannot be ruled out. Further, wildlife professionals should educate the public about evolutionary aspects of introductions and translocations, including hybridization and introgression.

Key words: hybridization, introduced species, introgression

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Three escalating phenomena - species introductions, modification, and fragmentation - break down reproductive isolation among many animal and plant species (Rhymer & Simberloff 1996). Although hybridization has been cited occasionally as threatening genetic integrity of species (e.g. Johnsgard 1961), it has not been widely seen as a major conservation problem, except perhaps for fishes: releases of bait species and transplants for sport-fishing and stock enhancement have generated concern (e.g. Verspoor & Hammar 1991).

The same problems beset mammals and birds. Hybridization is increasingly detected as new molecular methods often show hybridization when morphology does not. Allozymes, amplified polymorphic DNA (RAPDs), microsatellite DNA, and single-copy nuclear DNA all trace descent of nuclear markers (Avise 1994). Because mitochondrial DNA (mtDNA) is maternally inherited, if mtDNA haplotypes are restricted to different populations, they can indicate the direction of hybridization. A full analysis of hybridization requires both nuclear markers and mtDNA (Campton 1990).

Matings between species, between subspecies, and even between individuals of genetically distinct populations with no separate taxonomic status are all hybridizations. 'Introgression', gene flow between populations, occurs when hybrids backcross to parental populations (Anderson 1949). A hybrid swarm contains individuals of various hybrid and backcross generations. It is arbitrary at which point an individual is viewed as a hybrid as opposed to a member of a parental population who has acquired some genes through introgression (Verspoor & Hammar 1991).

The extent of hybridization in the wild

Both recent molecular studies and much older literature depict widespread animal hybridization (Raven 1976, Templeton 1989). For example, among galliforms, grouse and quail frequently hybridize with each other or with closely related subspecies (Johnsgard 1973). Many crosses have been recorded in the laboratory, but some occur in nature. For instance, introductions of the northern bobwhite quail *Colinus virginianus* into the Pacific

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Northwest and of the northern bobwhite and California quail *Callipepla californica* into Utah have led to hybridization between these two species in the field and in captivity. Within species, massive introductions, reintroductions, and transplantations of various bobwhite quail subspecies throughout the United States (Long 1981) have apparently combined with the release of pen-raised quail (Gutiérrez 1993) to produce extensive hybridization. Many waterfowl hybridize readily (Johnsgard 1968); over 400 types of interspecific hybrids are known (Gray 1958). Most bizarre pairings occur in captivity, but some crosses involving introduced species are found in the wild, as will be discussed below. Hybridization is also common among mammals in nature (Gray 1972). For example, among mustelids, hybrids of sable *Martes zibellina* and pine marten *M. martes* are common (Grakov 1994), while the European polecat *Mustela putorius* and the steppe polecat *M. eversmanni* hybridize where they are sympatric (Lynch 1995).

The importance of hybridization in wildlife populations

Hybridization does not necessarily mean that a parental taxon is genetically threatened. Hybridizations can fail to produce offspring - as do those between European mink *Mustela lutreola* and introduced American mink *M. vison* (Rozhnov 1993). Or the offspring can be sterile - as are almost all those between donkeys *Equus asinus* and Burchell's zebra *E. burchelli* (Gray 1972), or between the red hartebeest *Alcelaphus buselaphus* and the blesbok *Damaliscus dorcas phillipsi* (Robinson & Morris 1991). Or one sex of the F_1 hybrids - generally the heterogametic sex - can be sterile (Haldane 1922). Or the introgression can occur wholly or largely in one direction. For example, genes of introduced rainbow trout *Oncorhynchus mykiss* have introgressed into the threatened native Apache trout *O. apache* in the American Southwest, but not vice versa.

Even if introgression occurs, it can be restricted. Sometimes a narrow, stable hybrid zone arises, with introgression sharply reduced beyond the zone and neither parental gene pool greatly modified (Harrison 1993). I know of no clearcut example with an introduced species, but in many instances species mix and hybridize because of habitat change, and a stable hybrid zone results. For example, several bird species and subspecies were largely allopatric on either side of the North American Great Plains after forest retreat during the Pleistocene. These are now in secondary contact because of fire control and planted trees (Samson & Knopf 1994). Several of these pairs of species and subspecies form stable, narrow hybrid zones, e.g. red- and yellow-shafted flickers *Colaptes auratus cafer* and *C.a. auratus* respectively (Moore & Price 1993). There is no reason to think that the same forces cause all hybrid zones (Harrison 1993). At least some such zones may be maintained by lower hybrid fitness combined with frequent interbreeding at the point of contact.

Hybridization can be rare because parental individuals are rarely in contact. In galliforms, for example, much reproductive isolation is achieved by different habitat preferences (R. Gutiérrez, pers. comm.), and some hybridizations have increased in frequency because of land-use changes and habitat destruction. Some of these are of species of conservation concern. The greater prairie chicken *Tympanuchus cupido pinnatus* and sharp-tailed grouse *T. phasianellus* are both threatened in Colorado and hybridize more often (with fertile F_1) because changing land use has lessened habitat separation, but massive introgression is not evident (Ellsworth et al. 1994, C. Braun, pers. comm.). These hybrids seem to be at a mating disadvantage with respect to parentals (Johnsgard 1973).

However, with or without introgression, hybridization can threaten a taxon's existence.

Introgression and changing gene pools

Birds

Mallards *Anas platyrhynchos* have hybridized with ca 40 other species (Johnsgard 1968). Introduced mallards have hybridized with indigenous ducks in New Zealand, Hawaii, Australia, and Florida, while anthropogenic habitat change has fostered mallard range expansion that led to introgressive hybridization with the American black duck *A. rubripes* in the Northeast and the Mexican duck *A. platyrhynchos diazi* in the Southwest (references in Rhymer & Simberloff 1996). Mallard introductions on islands have been particularly threatening. Hybridization with mallards threatens the New Zealand grey duck *A. superciliosa superciliosa* (Rhymer et al. 1994) and the Hawaiian duck *A. wyvilliana* (Griffin et al. 1989). In the Mariana islands, a hybrid swarm resulted from interbreeding by mallards (probably stragglers) with an endemic race of the Pacific spot-billed duck *A. poecilorhyncha* (Yamashina 1948), but this swarm is now extinct, replaced by mallards (Reichel & Lemke 1994). In Florida, migratory mallards fly north to breed, but domesticated non-migratory individuals that escaped or were released threaten the endemic Florida mottled duck *A. fulvigula fulvigula* by hybridization (Mazourek & Gray 1994).

Introductions in one area can lead to hybridization elsewhere. Habitat destruction and hunting reduced the white-headed duck *Oxyura leucocephala*, originally a widespread Mediterranean species, to just 22 individuals

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in southern Spain, but a recovery program allowed this population to reach nearly 800 (Anon. 1993, Waite 1993). Meanwhile, the ruddy duck *O. jamaicensis*, reared in captivity in England as an exotic amenity, escaped and invaded the Continent, including Spain (Owen et al. 1986, Waite 1993). Its numbers greatly exceed those of its congener, and at least 10 fertile hybrids have now hatched in nature (Waite 1993).

In Germany, the introduced North American Canada goose *Branta canadensis* is hybridizing with the native greylag goose *Anser anser* (Gebhardt 1996). Introduced doves also hybridize with indigenous congeners. In South Africa the introduced Mozambican red-eyed dove *Streptopelia semitorquata semitorquata* has produced a hybrid swarm with the declining endemic subspecies *S.s. australis* (Brooke et al. 1986). Introduced Madagascan turtle doves *S. picturata picturata* have similarly produced a hybrid swarm in the Seychelles with the indigenous *S.p. rostrata* (Cade 1983).

Two New Zealand projects to save restricted island endemics were threatened by introgression. One female of the minuscule population of the black robin *Petroica traversi* mated with a Chatham Island tit *P. macrocephala chathamensis*, producing a female offspring that was destroyed as a threat to the species (Butler & Merton 1992). Red-crowned and yellow-crowned parakeets *Cyanoramphus novaezelandiae* and *C. auriceps*, respectively, have been mated in captivity and hybrids released. They may spread to other sites, including islands where the two species co-occur with low levels of natural hybridization, and introgression could destroy traits that isolate them (Towns et al. 1990).

Mammals

Canada established the Wood Buffalo National Park in 1922 to protect the dwindling population of wood bison *Bison bison athabascae*. But over 6,000 plains bison *B.b. bison* from southern Alberta, released in the park, massively interbred with the much smaller wood bison population (Middleton & Liittschwager 1994). A small isolated herd founded new populations, including one transplanted to the Elk Island National Park that is apparently genetically pure (Peden & Kraay 1979). Recovery of the wisent *Bison bonasus* in Europe was also threatened by hybridization with plains bison. The wisent herd at the Caucasus National Park has plains bison genes because of an attempt in the 1920s to improve what was perceived to be a failing European stock (Fisher et al. 1969).

Two major American endangered species rehabilitation campaigns are compromised by introgression. The Florida panther *Felis concolor coryi*, which has declined to about 40 individuals, has been the target of an expensive, controversial project (Rhymer & Simberloff 1996). After much concern about impending 'miscegenation' with Texas cougars *F.c. stanleyana* and 'contaminated bloodlines' (Cristoffer & Eisenberg 1985, p. 9), the Florida panther was discovered to have already been contaminated (O'Brien et al. 1990). One entire population consists of hybrids between the Florida panther and unknown Latin American subspecies released by public wild-animal attractions. Another population contains individuals with these hybrid traits, and occasional movement occurs between the two groups. Eight Texas cougar females have recently been released in Florida in the face of this *fait accompli* plus concern about inbreeding depression (Maehr & Caddick 1995).

The red wolf *Canis rufus* reintroduction in the eastern United States (Warren 1994) is also problematic. First, there is controversy about whether the red wolf originated by hybridization between the grey wolf *C. lupus* and coyote *C. latrans* (references in Rhymer & Simberloff 1996). Second, even if the red wolf does not have a hybrid origin, it will encounter burgeoning coyote populations anywhere it might be reintroduced. MtDNA analysis shows that many individuals from its historical range have either grey wolf or coyote haplotypes (Wayne & Jenks 1991), and a hybridization between a coyote and a translocated red wolf has been reported (R. Wayne, pers. comm.).

Grey wolf populations have been modified in Europe (Butler 1994), the United States (Hill 1993, Hope 1994), and probably the Middle East (Horwitz 1995) by hybridization and introgression with domestic and feral dogs *C. familiaris*. However, sympatry does not automatically lead to such introgression into the wolf, as indicated by a mitochondrial DNA analysis in Italy (Randi et al. 1995). Domestic dogs also hybridize and introgress with the imperilled Ethiopian simien jackal *C. simensis*, a process facilitated because dogs outnumber jackals ten to one (Gotelli et al. 1994). Hybridization with feral housecats *Felis catus* threatens the genetic integrity of both European wildcats *F. silvestris* (Hubbard et al. 1992) and African wildcats *F. libyca* (Stuart & Stuart 1991), with introgression detected even in remote regions.

Hybridization abounds among ungulates. Japanese Sika deer *Cervus nippon nippon* introduced to Scotland about 80 years ago may threaten the genetic integrity of the native red deer *C. elaphus* by hybridization and introgression (Abernethy 1994). Sika deer were also introduced to Ireland (Harrington 1973, 1982). The only native red deer in Ireland are in County Kerry, and hybridization has not been confirmed there despite the presence of Sika deer in the national park. Hybridization is common in other counties where red deer are introduced (Harrington 1973, D.P. Sleeman, pers. comm.). In Ireland, native red deer have also been interbred with American wapiti *C. canadensis* with introgression evident from

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morphology (Fairley 1975). In Texas, white-tailed deer *Odocoileus virginianus* and mule deer *O. hemionus* hybridize, occasionally producing viable, fertile offspring (Carr et al. 1986). Introgression is primarily into the mule deer population and may aid local displacement of the latter by white-tailed deer. In South Africa, hybridization with the native gemsbok *O. gazella* occurred following introduction of scimitar-horned oryx *Oryx dammah* (Brooke et al. 1986). Translocations of naturally allopatric blue wildebeest *Connochaetes taurinus* and black wildebeest *C. gnou* into one another's ranges has led to much interbreeding, as have numerous translocations of the subspecifically distinct bontebok *Damaliscus dorcas dorcas* and blesbok (Brooke et al. 1986). Many populations of springbok *Antidorcas marsupialis* and impala *Aepyceros melampus* that were probably genetically distinct have been mixed by translocation (Brooke et al. 1986).

Even the reintroduction of Przewalski's horse *Equus przewalskii* to the Mongolian steppe may already be compromised. In captive European herds, a domestic mare *E. caballus* used as a foster mother bred with a Przewalski's stallion. This female is one of the 13 progenitors of the reintroduced herd (Bouman & Bouman 1994). Further such matings may also occur on the steppe.

Free-living swine in the United States consist of feral domestic hogs *Sus scrofa domesticus*, several introduced European wild boar *S.s. scrofa* subspecies, and hybrids of various generations between the two (Mayer & Brisbin 1991). Because hunters increasingly want European wild boar, there have been many introductions, as well as translocations among the states. Hybridization and introgression are frequent between feral domestic individuals and wild boar, so there are regional hybrid swarms. Introgression of wild boar genes may partly cause habitat shifts in wild swine.

Before the introduced brown hare *Lepus europaeus* drove the native arctic hare *L. timidus* into allotropy in Sweden, extensive hybridization was reported (Siivonen 1972). Apparently the earlier rut of the brown hare allowed brown hare males to court arctic hare females. The extent of introgression must be determined by molecular means.

Problems in the absence of introgression

Even without introgression, hybridization can threaten a species. The declining European mink population hybridizes with introduced American mink (Rokos 1993, Rozhnov 1993). American mink become sexually active earlier than European mink and are larger. Thus American mink males mate with European mink females as the latter come into oestrus. These impregnated females then repel other males, resorb embryos and leave no offspring that year. American mink reproduction and recruitment proceed normally. It is ironic that the American mink was introduced to the ex-Soviet Union in the belief that hybridization would produce a valuable furbearer (Rokos 1993). A similar problem may befall the Cape mountain zebra *Equus zebra zebra*, whose crosses with feral donkeys *E. asinus*, facilitated by fragmentation of the zebra population, produce sterile mules but lower zebra productivity (Breytenbach 1986, Brooke et al. 1986).

Racial purity and other non-biological concerns

Should introgressive modification of gene pools worry conservationists? If I were dealing with humans and had written 'miscegenation', my concerns would have resembled a brief for racial purity. James (1980) ridicules the brouhaha over introgression in the dusky seaside sparrow *Ammodramus maritimus nigrescens* on these grounds. Racist literature often inveighs against intermarriage because it homogenizes gene pools. If we reject this reasoning for humans, should we care about analogous phenomena in wildlife? Does it matter if infraspecific entities such as subspecies and races are homogenized? Few published arguments for preserving infraspecific entities use racist imagery. When one does, we are taken aback, as when Lever (1987) writes of mallards, "The adulteration of the blood of a native species by that of a genetically superior alien is always to be deplored" (p. 44).

Conservationists are schizophrenic about race. On the one hand, the existence of genetically distinct populations has fostered concern for infraspecific entities; even the US Endangered Species Act allows endangered status for 'subspecies' and 'distinct population segments' (US Fish and Wildlife Service 1988, Hill 1993). On the other hand, I doubt that many conservationists worry about mixing human races. One can simply declare that it is proper to designate races for other species and so to be concerned for their survival but not for humans. Thus, Gould (1985) rationalizes this stance on the grounds that humans move and interbreed more than other species do. One would expect a decision about whether a species has races to rest on geographic patterns of genetic variation *per se*, not on mechanisms that might have generated them. Another rationale for thinking differently about humans than about other animals is implied by Carr & Dodd (1983), who suggest that introgressive hybridization in sea turtles is imposed by human activities, so humans are morally obliged to act against it. The fact that humans generally choose their mates is probably one reason why conservationists do not deplore interracial marriage.

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The obligations of wildlife biologists and managers

Whatever the reason we deplore the extinction of species, we should abhor species loss by reproductive wastage to intersterile matings with another taxon. We should thus not introduce species that pose this threat, and we should attempt to eliminate or to reduce populations that are already present and causing the problem. If such measures are impractical, as for the American mink in Europe, a translocation of the threatened native species to an exotic-free area may be the only solution, but only with assurance that the translocation would not threaten species of the target area. For example, the European mink was released on Valaam Island in Lake Ladozhskoe, wholly within its range, with no evident problems for resident species (Tumanov & Rozhnov 1993).

If introgression is the threat, whether we should do anything is not so clear. As noted above, some would argue that it behooves humans to attempt to fix any problem they cause, but surely in an era of limited resources, some cases of genetic introgression simply do not warrant action.

Introgression can lead to outbreeding depression - lowered fitness in F_1 or later generation hybrids, sometimes to the extent that a population is lost, as in the Tatra Mountain ibex *Capra ibex ibex* in the former Czechoslovakia after breeding with introduced individuals (Templeton 1986). Outbreeding depression can be so severe that a hybrid is unfit in any environment. Other times loss of coadapted gene complexes specifically adapted to a locale lowers fitness, as in orientation behaviour of local populations of salmonid fishes (Allendorf & Waples 1995). A major recent theme in evolutionary biology is the discovery of vast amounts of interpopulational genetic differentiation, but it is controversial whether much of it reflects local adaptation, which can be determined only by intensive field study.

The prudent approach given such uncertainty is *not* to introduce exotic species. And one ought *not* to translocate or mix conspecific populations unless there is a real threat of population extinction without it; even then, one must consider the possibility that translocated and/or hybridized individuals might move to other areas.

Sometimes hybrids and backcrosses are as fit as parental populations, e.g. hybrids between mallards and New Zealand grey ducks (Haddon 1984). Such cases may be most troubling, as one instinctively feels that a population with genetically based morphological distinctness deserves protection, whatever its taxonomic status and even if its hybrids are fit. A recent US National Research Council committee concluded that any "evolutionary unit" comprising "a group of organisms that represents a segment of biological diversity that shares evolutionary lineage and contains the potential for a unique evolutionary future" deserves protection (N.R.C. 1995). The New Zealand duck fits this category, but the wording can easily be construed simply as an appeal to racial purity. Perhaps the best I can do is to say that, for whatever reasons - both utilitarian and moral - we prize natural variety, we should strive to protect it from anthropogenic assaults on integral gene pools.

If introgression occurs because of natural range expansion, there is little ethical or practical reason to attempt to stop it. Even if the range change is anthropogenic, the sympatry may be a *fait accompli* and there is no way to redress it. For example, the blue-winged warbler *Vermivora pinus* is expanding northward in North America, contacting the golden-winged warbler *V. chrysoptera*. Hybridization and introgression have contributed to the decline of the latter species (Confer 1992). The range of the blue-winged warbler is changing partly because of human land-use, but the scale is so great that there is no way to eliminate blue-winged warblers from the range of the golden-winged warbler. Nor is there any 'safe' site to which the golden-winged warbler can be translocated without other impacts on the environment.

Other times, as in the cases of the dusky seaside sparrow and the Florida panther, introgression is generated by conservationists who wish to introduce non-indigenous subspecies because the native one may not persist. If the threat is really this dire, it would be counterproductive to stop the translocation on grounds of loss of a local gene pool - the gene pool would be lost anyway. However, the example of the Tatra Mountain ibex should serve as a warning that the cure may be worse than the disease. Also, the contention that a population is too small to be viable is often just an opinion; some very small populations persist indefinitely (e.g. Walter 1990).

Various introduction, stock enhancement, and translocation programs should be re-evaluated in light of introgression. Even such well-meaning actions as translocations of endangered marine turtles can cause breakdown of local adaptations (Carr & Dodd 1983) and gene flow between genera separated evolutionarily by tens of millions of years (Karl et al. 1995). The alarm has been raised for fisheries (e.g. Allendorf & Waples 1995) but not frequently for game animals. Kozicky (1993, p. 6), for example, proposes massive release of pen-raised quail without mentioning any of the problems I have listed here. As Gutiérrez (1993) notes, there is little study of any aspect of the genetic relationship of pen-reared and wild quail, and large-scale current and proposed releases may be detrimental. Genetic analysis is long overdue for releases of pen-reared birds and translocation programs for quail. Wildlife managers and commissions should educate hunters about potential problems with introductions and translocation, including hybridization. After all, the hunting public, eager for bigger, better, and more game, ex-

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erts political pressure that often motivates introduction and translocation programs or simply freelances a project without governmental control. However, wildlife biologists usually give evolution short shrift in comparison to ecology.

Culling is often proposed for managing hybridization and introgression problems. For example, massive shooting of hybrids has been used to reduce the threat of introgression between ruddy and white-headed ducks in Spain (Waite 1993) and between yellow-crowned and red-fronted parakeets in the Chatham Islands (Cade 1983). In New Zealand, where both wapiti and red deer are introduced, intensive shooting from helicopters of red deer and hybrids was used to try to preserve a 'pure' wapiti herd (Challies 1995). Fairley (1975) suggests local extermination of sika deer in Ireland to preserve the native red deer gene pool. Two considerations suggest caution. First, morphology does not always indicate hybrid individuals. Second, if the population to be 'rescued' from genetic extinction is very small, unique genes that we want to save may be largely contained in hybrids.

Conclusion

Hybridization with introduced species, with or without introgression, is a major conservation problem, especially when there is great disparity between population sizes of hybridizing taxa. Molecular techniques that unambiguously indicate introgression are new, so the known problems are but a sample of the existing ones. Further, the problems discussed here do not exhaust the possible bad outcomes of hybridization with introduced species. For example, in both frogs (Arano et al. 1995) and plants (Thompson 1991), introduced species have hybridized with native ones to produce invasive pest species.

Introductions should be avoided for these reasons and for ecological ones, and translocations should be considered with a jaundiced eye. Especially for introgression at the infraspecific level, utilitarian and ethical considerations may not convince everyone there is a problem, but conservation biologists agree that infraspecific entities with independent evolutionary trajectories deserve protection, and this means protection from introgression as from other threats. Remedying a hybridization or introgression problem is often not trivial, short of eradication of the introduced taxon, and even this step may not suffice if the introgression has already happened. If culling of hybrids is used to prevent backcrossing into a threatened parental taxon, it is important to be able to recognize most hybrid individuals, which may not be possible morphologically. The greatest action that wildlife professionals can take to alleviate hybridization problems is to educate the public about genetic and evolutionary aspects of introductions and translocations.

Acknowledgements - R.J. Gutiérrez and J.M. Rhymer provided numerous helpful comments on this manuscript, and P. Nummi and D.P. Sleeman suggested important references. I thank the Organisation for Economic Co-operation and Development for supporting my participation in this project.

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