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S33-4 Extinction by hybridization and introgression in anatine ducks

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Abstract Non-indigenous species can bring about a form of extinction in native fauna through hybridization and introgression, as a result of human introduction or habitat modification bringing previously isolated species into contact. This process can be especially difficult for rare species that are brought into contact with congeners that are more abundant and aggressive. The best-known examples among the Anatinae involve the ubiquitous releases of mallard (*Anas platyrhynchos*) and its subsequent hybridization with the American black duck (*A. rubripes*), Florida mottled duck (*A. fulvigula*), and Hawaiian duck (*A. wyvilliana*) in North America, and gray duck (*A. superciliosa*) in New Zealand and Australia. Similarly, invasion of the European continent by escaped, captive-reared American ruddy ducks (*Oxyura jamaicensis*) has contributed to regional declines in the endangered white-headed duck (*O. leucocephala*). Use of molecular technology focuses attention on the extent of this under-appreciated problem that is not always apparent from morphological observations alone. Although some degree of gene flow is a normal, evolutionarily constructive process, hybridization with or without introgression may, nevertheless, threaten the genetic integrity and fitness, and so existence, of rare species.

Key words Introgressive hybridization, Introduced species, Genetic mixing, Extinction, Anatine ducks

1 Introduction

The most often cited causes of extinction are habitat destruction and/or fragmentation, cascade effects, overkilling and the impact of introduced species. The impact of introduced species is usually approached from an ecological perspective, involving such negative effects as predation or competition. Another negative impact, often overlooked but also important, is hybridization and introgression, which can dissipate the unique gene pools of native taxa and, in effect, exterminate them (Rhymer and Simberloff, 1996). Modification of gene pools via hybridization can occur through purposeful or accidental introductions of exotic species, or through habitat changes that bring previously isolated native species into contact. Once this has happened, the risk of genetic extinction then depends on the strength (or weakness) of reproductive barriers between taxa, the vigor and fertility of hybrids, relative and absolute sizes of parental populations, and relative competitive ability (Levin, 2002).

For the purpose of this study, hybridization is defined as the interbreeding of individuals from genetically distinct populations irrespective of taxonomic status, and introgression as gene flow (genetic mixing) between populations whose individuals hybridize. Identification of hybrids based only on morphological analyses can be quite difficult because, after several generations of backcrossing, phenotypes of hybrids tend to converge on those of the parental species (Rhymer et al., 1994). Genetic analyses are required to unequivocally identify all hybrid individuals. The direction of hybridization can be determined using mitochondrial DNA (mtDNA) analysis. mtDNA is inherited only from the female parent, so it is possible to trace taxic and sexual inputs into the parentage of hybrids, that is, whether matings occur consistently between the females of one species and males of the other, or in both directions (Rhymer et al., 1994). To determine the extent of introgression, analysis of bi-parentally inherited nuclear DNA markers, such as microsatellites, is required.

Recognizing that introgressive hybridization can also be an evolutionarily constructive process (Arnold, 1997), Allendorf et al. (2001) distinguished between natural forms of hybridization in wild populations and those that have been induced by anthropogenic activities. Here only anthropogenically-induced hybridization in anatine ducks is considered.

2 Hybridization through introductions

Taxic mixing resulting from animal introductions can be purposeful or accidental. Extensive hybridization between the endangered European white-headed duck (*Oxyura leucocephala*) and American ruddy duck (*O. jamaicensis*), for example, was initiated by the accidental escape of ruddy ducks from captivity in Britain, with near disastrous results (Hughes, 1996). On the other hand, mallard (*Anas platyrhynchos*) introductions have been purposeful and extensive throughout the world, contributing to the decline of closely related native species in North America, Hawaii, New Zealand, South Africa, and Madagascar. Hybridization with mallards has been implicated in the decline of American black ducks (*A. rubripes*) in eastern North America (Kirby et al., 2001). Purposeful introductions of mallards for hunting, in addition to changing land use, have brought these two previously isolated

species into contact (Callaghan and Kirby, 1996).

In southern Florida, escaped mallards from parks, backyard ponds and hunting clubs have hybridized with the mottled duck (*A. fulvigula*) to such an extent that the public is being warned that this could lead to the demise of their indigenous species (Mazourek and Gray, 1994). Another example is the endangered Hawaiian duck (*A. wyvilliana*) or koloa, which is threatened by hybridization with released mallards such that the population on Kauai is now the only one remaining unimplicated in a hybrid swarm (Rhymer, 2001).

In New Zealand, the gray duck (*A. superciliosa superciliosa*) was considered a game species until the 1990s, but is now listed as endangered. It is on the verge of disappearing as a distinct species, due to introgressive hybridization with introduced mallards (Williams and Basse, 2006). There is concern in Australia that a similar situation could develop for the gray (Pacific black) duck there. Meller's duck (*A. melleri*), an endangered species endemic to Madagascar, is also threatened by hybridization with game-farm mallards kept by indigenous people on Lac Alaotra, the primary location for Meller's duck (Young and Rhymer, 1998). Mallards have been introduced both deliberately and accidentally into South Africa as well, threatening the integrity of the yellow-billed duck (*A. undulata*) through extensive hybridization (Cape Nature Conservation, 1994; Owen et al., 2002).

3 Hybridization through habitat change

Changing land use practices in the southwestern United States facilitated contact between mallards and the Mexican duck (*A. diazi*) (Hubbard, 1977). Extensive hybridization between these taxa well into northern Mexico led to the Mexican duck being determined as conspecific with the mallard in 1983 (AOU, 1983), preventing its listing as endangered. This decision was made despite the fact that pure populations of Mexican ducks remain in central Mexico and that the species is as distinct genetically from the mallard as other recognized species in the complex in North America (McCracken et al., 2001; Rhymer, unpubl. data). Habitat change due to agricultural expansion and increased urbanization has also contributed to the exposure of the American black duck to mallards (Johnsgard and Disilvestro, 1976; Heusmann 1974, 1988).

4 Mechanism of decline

Hybridization can lead to the decline of species through either outbreeding depression or genetic mixing and consequent genic dilution and dispersion. Outbreeding depression is expressed in lowered fitness in offspring and can arise whether hybrids survive or not. Low survivorship results either from embryonic inviability (one or both sexes) or the inability of young to cope with local environmental conditions. Even if hybrids do survive well, they may be sterile or the offspring of one cross or the other may be sterile. Thus, hybridization with or without introgression can contribute to extinction of rare species, because relatively more reproductive effort is dissipated in hybrid matings (Fig. 1). This phenomenon led Wolf et al. (2001) to declare that "hybridization is the most rapidly acting genetic threat to endangered [plant] species, with extinction often taking place in less than five generations".

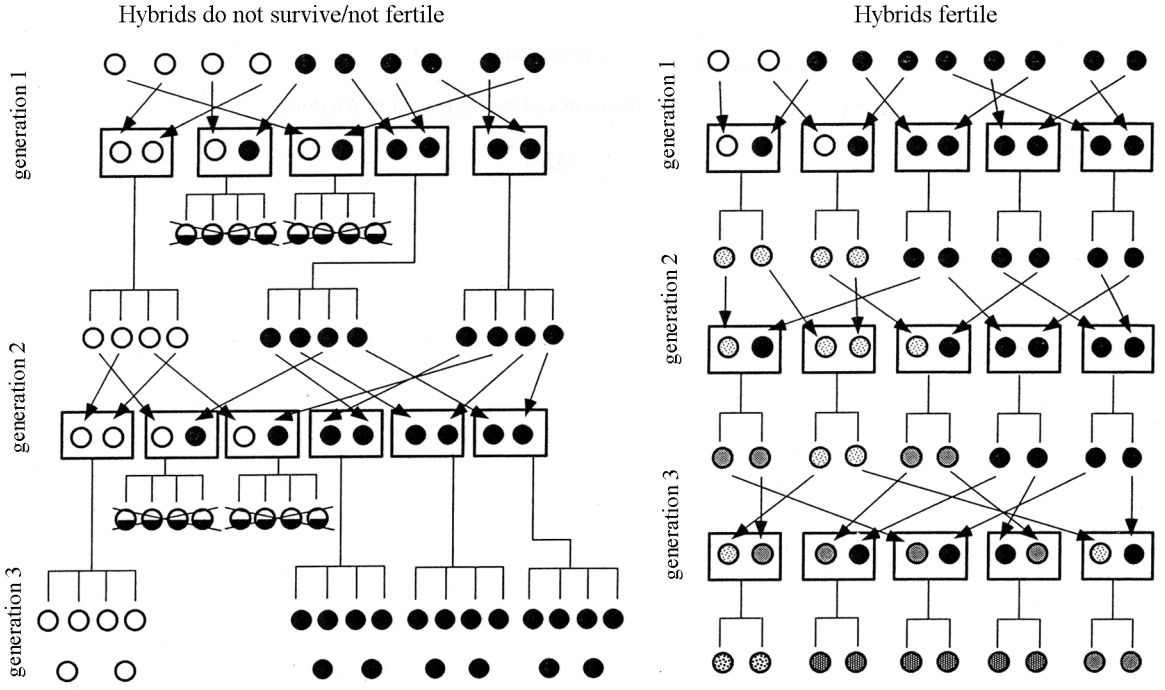

Fig. 1 Hybridization can lead to the decline of the rarer species (white circles) whether it results in fertile offspring or not
Left: although the number of individuals has increased after three generations, the proportion of the rarer species has declined. Right: a hypothetical example in which hybrids are fully viable and fertile, and form a hybrid swarm with complete genetic mixing (after Levin, 2002).

5 Solving the problem

Helbig et al. (2002) discuss the taxonomic implications of hybridization due to secondary contact, suggesting that taxa should be considered as separate species if the level of divergence between them indicates that they will remain distinct. The example given is the ruddy duck and white-headed duck. Unfortunately, even highly divergent congeneric species are capable of forming a fertile hybrid with complete admixture, despite being separated for long periods of time (Price, 2002). The retained ability of taxa to hybridize and introgress is not indicative of conspecificity. Rather, the emphasis should be put on protecting species, especially rare species, from the hazards of hybridization.

Possible solutions are the isolation or translocation of endangered species or the culling of hybrids. The former is often impractical and care must be taken to ensure that species are not being relocated to environments to which they are not adapted. This approach has been suggested for the Laysan duck (Rhymer, 2001) and gray duck (Rhymer, et al., 2004), but careful consideration of the consequences is essential. Culling ruddy ducks has been recommended to control the increase in hybridization between this species and the white-headed duck (Hughes et al., 1999, 2006).

In some cases, it will ideal to cull hybrids as well, but they may contain some of the last remaining genetic record of a species on the verge of extinction. As a last resort, hybridization with a closely related subspecies could even be used to help salvage distinctive characteristics, as has been done with the Florida panther (*Felis concolor*) (Hedrick, 2001). Allendorf et al. (2001) recommended protecting anthropogenic hybrids when they contain the only remaining genetic information of a taxon otherwise lost through genetic mixing, as well as taxa that have arisen through natural hybridization.

Thus, when planning translocations and reintroductions, it is essential to heighten awareness of possible deleterious consequences to prevent possible extinctions of native species through hybridization and introgression.

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