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Introduced populations of birds and mammals may have genetic characteristics differing from those of naturally occurring populations. Such populations are often created by translocation of small numbers of individuals. This leads to founder effects and subsequent genetic drift, often resulting in larger differences in allozyme patterns between introduced populations than between naturally established populations. In many cases, a large proportion of alleles has been lost a few generations after the introduction. Under certain conditions, the mean level of heterozygosity is also severely reduced. Theoretically, a reduction in the number of alleles in a population will result in a lowered potential to track environmental changes, but there is scant evidence for this in introduced wildlife. Likewise, evidence is lacking for inbreeding depression occurring in introduced populations of birds and mammals in the wild. Finally, some conclusions are drawn concerning management strategies for wildlife introductions with respect to genetic considerations.

Key words: Wildlife, species introductions, genetic variability, number of alleles, heterozygosity, founder effects, inbreeding

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Whether we try to manage, eradicate or limit the numbers of introduced wildlife populations, we need to recognise that they may have genetic characteristics that differ from naturally occurring populations of the same species.

The amount of genetic variability present in a population is important for its ability to survive and evolve. Populations founded by small numbers of individuals are expected to have reduced genetic variation, which also has been shown to be the case (Berry 1986). This is not less so for introduced populations. Founding numbers of such populations have often been small, and their genetic variability therefore reduced.

Many wildlife introductions and reintroductions that have been performed with very small founding groups have nevertheless been successful. Some examples are the red-necked wallaby *Macropus rufogriseus* in Scotland (Clutton-Brock 1992, Weir et al. 1995), feral horses *Equus caballus* in South America (Clutton-Brock 1992), the beaver *Castor fiber* in Sweden (Hartman 1994), the Canada goose *Branta canadensis* in northern Europe (Fabricius 1983), and the white-tailed deer *Odocoileus virginianus* in Finland (Nummi 1996).

Intraspecific genetic variability is partitioned between populations and between individuals in a population. The degree of differentiation between populations is commonly measured using genetic distance (Rogers 1972, Nei 1978) or related variables, based on allozyme frequencies or morphometric characters. Within a population, genetic variability can be measured as the average number of alleles present for a particular locus or for a number of loci (Leberg 1990). Indirect estimates of the magnitude of allelic diversity can be found in the degree of DNA fingerprint variability. The variation within a population can also be measured as the average proportion per individual of certain loci that are heterozygous. Mean heterozygosity is determined by the allele diversity, the amount of inbreeding, and the type and intensity of natural selection (Young et al. 1996).

The term 'introduced species' will be used to refer to species that were established in new geographic environments through translocations by man. However, many aspects of species introductions will be similar to translocations leading to 'reintroductions of species' (Wolf et al. 1996). In many cases, the distinction between 'introduction' and 'reintroduction' is blurred, as translocated individuals originate from a different area and may be genetically different from those originally occurring in the target area. When the beaver was reintroduced into Finland, a large part of the translocated individuals belonged to another species, the American beaver *Castor canaden-*

sis, and not to the original European species (Lahti & Helminen 1974).

Wildlife species have been deliberately introduced for many different purposes, but also inadvertently. In this context, the term 'wildlife' covers all species of birds and mammals, irrespective of whether they are utilised by man or not.

This review is affected by the anecdotal character of the data and by the lack of documentation of all failed introductions. Wolf et al. (1996) showed that translocations of species to areas outside their historical distribution range (or to its periphery) are less successful than introductions into core areas. One important factor contributing significantly to the success of translocations of birds and mammals is the number of individuals released (Wolf et al. 1996). In some cases, the establishment of exotic bird and mammal species does not take place until after a series of failed attempts of introduction, e.g. the starling *Sturnus vulgaris* in North America (Pimm 1991).

The purpose of this paper is to review the evidence for genetic impoverishment in introduced wildlife populations, and to interpret the ecologic and evolutionary consequences of such impoverishment. However, there are relatively few experiments with wildlife introductions where the population genetic consequences have been carefully documented, so I include several examples dealing with fish or insects, where the effects of introductions were simulated.

First, I discuss how introductions may affect genetic variability between populations. Secondly, I evaluate the consequences of introductions for genetic variability within populations. There, I present predictions for the genetic variability of establishing new populations through the colonisation by small groups of individuals. I then examine the evidence concerning genetic variability in introduced wildlife populations as compared to source populations or other naturally established populations. Next, I review the ecologic and evolutionary implications of the genetic characteristics in introduced wildlife populations. Finally, I discuss some conclusions that could form a basis for management recommendations.

Species introductions and genetic variability among populations

The size and composition of founding groups are crucial for the genetic characteristics and the genetic variation in new populations (Whitlock & McCauley 1990). This is of course true for naturally colonising as well as for introduced species. The selection of founders will have a major effect on the range of genetic variation that natural selection may act upon.

The establishment of new populations through introduction will be different from those resulting from spontaneous spread. The selection of individuals for introduction will often be random - or this was at least the case in earlier introductions. Alternatively, animals with preferred characteristics have been selected, depending on the purpose of the introduction. In natural colonisation events, certain segments of the population, e.g. those with an inherited tendency for dispersal, will most likely form the population propagules.

What is then the evidence for introduced populations showing different characteristics? The genetic structure of several bird species has been studied using protein electrophoresis. Genetic distances between populations founded by introductions were generally larger than those between natural populations (Ross 1983, Parkin & Cole 1985, Baker & Moeed 1987) although this was not always the case (Baker 1992). The increased inter-population differences may have been due to founding effects and genetic drift. In some cases, natural selection may have been responsible for observed differences between introduced populations (Baker & Moeed 1979).

The house mice *Mus musculus* introduced to the Faroe archipelago were studied by Berry et al. (1978) who found that all island 'races' were very distinct in allozyme patterns, morphometric traits and non-metric skeleton variation in spite of the relatively short time having passed since the introduction, in some cases less than 200 years. However, this period of time still corresponds to a fairly large number of generations, as the house mouse reaches sexual maturity at the age of 35-40 days (Reichstein 1978).

Alpine ibex *Capra ibex ibex* populations created by translocation also differed more from the source populations in allozyme patterns than did those created by natural dispersal (Scribner & Stüwe 1994). The reason for this, however, was not clear.

Populations established by introductions may, like any isolated population founded by a small number of individuals, rapidly evolve to what has been called 'instant subspeciation' (e.g. Berry 1986). Populations may differ in which characters have been fixed by founding effects and by genetic drift, and this may lead to differences in survival and reproduction between populations.

Species introductions and genetic variability within populations

Predictions

In the founding of new populations a number of alleles, especially the rarer ones, are expected to be lost in the founding event itself (Wright 1931, Nei et al. 1975). In the absence of selection, they may also be lost due to ge-

netic drift in the period of low numbers of individuals following establishment. In a study based on enzyme electrophoresis, Leberg (1992) founded a number of populations of the eastern mosquitofish *Gambusia holbrooki*, and found that 30% of alleles were lost in a single bottleneck-experiment with six founders. For fish introductions, it has been recommended that at least 50 founding individuals be used in order to preserve allelic diversity (Allendorf & Ryman 1987).

A reduction in heterozygosity in introduced populations can be expected on theoretical grounds (Wright 1931, Nei et al. 1975, Howard 1993). If the effective number of founders is below 10 individuals, heterozygosity is predicted to decline by 5% or more compared to the original heterozygosity (Leberg 1990). However, a large degree of heterozygosity may still be preserved if there is a rapid increase in population size following the founding event (Nei et al. 1975). This phenomenon was observed in a newly founded fruit fly *Drosophila pseudoobscura* population in Colombia. The crucial point of the theoretical explanation of Nei et al. (1975) was that each founding individual carries a high degree of the original heterozygosity in the source population.

In the experimental mosquitofish populations studied by Leberg (1992), the levels of heterozygosity were reduced, especially in the populations with the smallest number of founding individuals (one pair). However, the effect of founding events on the level of heterozygosity was highly variable. Almost half the number of populations founded by six individuals (in one or two successive founding events) had higher estimates of heterozygosity than the source population (Leberg 1992).

It is important to note that the most likely effective number of founders is considerably lower than the number of individuals released (Leberg 1990). One reason for this is that the founding individuals are often closely related. When Canada geese were released in Sweden to establish new breeding colonies in the 1930s to 1980s, family groups were captured in one part of the country and released together in another area (G. Sjöberg, unpubl. data). In such cases, heterozygosity may be drastically reduced in the next generation.

Evidence in birds and mammals

Allelic diversity as well as mean levels of heterozygosity were lower in most introduced bird populations as compared to source populations or other natural reference populations (Parkin & Cole 1985, Baker & Moeed 1987, St Louis & Barlow 1988). In the starling, only allelic diversity was lower (Ross 1983).

In most island populations of mammals, many of which had been introduced, heterozygosity was considerably reduced, compared with mainland populations (Kilpatrick 1981). Heterozygosity was also lower in a bison *Bison bison* population founded by translocation of a small number of individuals, as compared to a more natural herd (McClenaghan et al. 1990). In Alpine ibex populations founded by reintroductions, or having gone through bottlenecks, there was a correspondence between the number of founders and the degree of heterozygosity (Scribner 1993).

Consequences for survival and reproduction

According to evolutionary theory (e.g. Nei et al. 1975), the potential to respond to natural selection will be low if the population contains a small number of alleles. The agents of selection may be the physical environment or interspecific interactions. Sufficient genetic variation may be necessary for long-term survival of the population (Berry & Bradshaw 1992). High variability in the major histocompatibility complex (MHC) was considered crucial for disease resistance at least in mammals by O'Brien et al. (1985) and O'Brien & Evermann (1988).

However, I know of no introduced wildlife population where a connection has been demonstrated between the number of founders, immunodefense variability, and mortality in epizootics. The Swedish Canada goose population was founded by probably only five individuals, has very low DNA fingerprint variability (Tegelström & Sjöberg 1995) and most likely little MHC variability. Antibodies from Sindbis-type virus were found (Lundström et al. 1992), but no epizootic has been reported in Canada geese in the Nordic countries (Heggberget 1991). The reintroduced Swedish beaver population as well as other European populations have extremely low MHC variability - but no reduced viability has been demonstrated (Ellegren et al. 1993).

One might speculate that, in the human-created landscape, where disturbance pattens are quite predictable, there may be less need for responding to frequent environmental shifts. Therefore, lack of allelic diversity may be less disadvantageous.

The fitness consequences of founding new populations with small numbers of individuals have not been studied in proper experiments with birds and mammals in the wild. However, they were studied in a cage experiment with a wild stock of African satyrine butterflies *Bicyclus anynana* by Brakefield & Saccheri (1994). Bottleneck lines were established from groups with different numbers (one, three and ten) of founding pairs, while control lines with a large number of individuals also were held.

In this experiment, 64% of 8th-generation females from single-pair lines were sterile, compared with 11% of those from the control group. Hatcheability of eggs was reduced by 50% or more in populations founded by single pairs, while it was not reduced in lines founded by 10

pairs. However, several single-pair lines had recovered the original egg viability in seven generations after the founding event. Results obtained from the founding events in this experiment also supported the hypothesis that some lines had been purged with respect to deleterious alleles (Brakefield & Saccheri 1994). The mechanisms behind this are not quite understood but unexpected phenomena have also been observed in other species after severe bottlenecks (e.g. Bryant et al. 1986, Carson 1990).

A decrease in heterozygosity leading to reduced rates of survival and reproduction is commonly referred to as 'inbreeding depression'. Two mechanisms are involved in this, but the effects of these cannot always be distinguished (Lacy 1993).

First, high levels of heterozygosity may directly lead to increased fitness (Lacy 1993), e.g. through balanced development. Some empirical evidence for this exists (Frelinger 1972, Quattro & Vrijenhoek 1989, Leberg 1990).

Secondly, high levels of homozygosity in a population where individuals sharing a common ancestry mate with each other result in a high percentage of individuals where rare recessive alleles are expressed in the phenotype (Allendorf & Ryman 1987, Lacy 1993). If recessive deleterious alleles are present in the population, reduced fecundity, fertility and survival will result. A 5% decline of heterozygosity is predicted to have negative fitness effects in a population (Ralls & Ballou 1983).

Pusey & Wolf (1996) argue that there is increasing evidence for inbreeding in the wild. Wildt et al. (1987) claimed that the reproductive function of wild felines was impaired in bottlenecked populations for either of the above reasons. This conclusion, however, has been questioned (e.g. Caughley 1994).

Lacy (1993) and Frankham (1995) concluded that inbreeding depression can lead to the extinction of wildlife populations. Such extinctions may be triggered by environmental variables (Frankham 1995). Interaction between inbreeding depression and the environment was demonstrated in an experiment carried out by Jiménez et al. (1994) who studied the condition and survival of inbred and non-inbred white-footed mice *Peromyscus leucopus noveboracensis*, released into the wild. Differences in survival were much more drastic in the wild than in the laboratory.

According to Shields (1993), however, the occurrence of inbreeding depression in wild populations has not been demonstrated unequivocally. The patterns of inbreeding and of inbreeding depression, are most likely quite complicated in bird and mammal populations (Rowley et al. 1993, Smith 1993). This also holds for the opposite mechanism, outbreeding depression - or the decrease in fitness in offspring from parents from genetically differentiated populations (Shields 1993, Pusey & Wolf 1996).

Previous adaptation to inbreeding

Populations purged from deleterious alleles may be suited for introduction as they may not be sensitive to further inbreeding (Leberg 1990). The butterfly experiment by Brakefield & Saccheri (1994) mentioned earlier suggests that the success of a colonising population could depend on its adaptation to a condition with low heterozygosity. However, the occurrence of deleterious alleles is stochastic and not predictable. Lacy (1993) reports on experiments on populations of old-field mice *Peromyscus polionotus*, that island populations that had gone through bottlenecks and that therefore showed much lower heterozygosity had as many deleterious alleles as the more diverse mainland populations.

Some breeding programmes suggest that it is feasible to adapt a wild species to inbreeding, as was shown in the Speke's gazelle *Gazella spekei* (Templeton & Read 1983). Many of the birds and mammals that were introduced most frequently by man were domesticated forms (Ebenhard 1988). One important part of the domestication process is a reduction in genetic variability including decreased heterozygosity (Berry 1969, Clutton-Brock 1992). In artificial breeding, the deletion of deleterious alleles is, of course, crucial.

Therefore, it seems likely that previous adaptation to small population size and a low degree of heterozygosity may have contributed to the success of introductions of domesticated species like goats, swines, and horses. This may also have contributed to the success of Canada geese (Fabricius 1983) in northern Europe during the last century, in spite of the very small number of introduced individuals. Canada geese were held in European parks from the 17th century onwards under near-domesticated conditions (Long 1981).

Conclusions

Following the predictions of genetic theory, basically two strategies can be deduced for planning wildlife introductions with respect to genetic considerations. The first one is to use a large group of individuals with a diverse genetic background. This means that the source population or populations should be as diverse as possible. Also, several source populations should preferably be used (Smith et al. 1975, Allendorf & Ryman 1987, Leberg 1990), as this should minimise the risk for low levels of heterozygosity, and provide the new population with a large number of alleles on which different, opposing factors can act. This strategy should be used when long-term survival is important, e.g for creating new populations of threatened species.

The second strategy is based on the use of individuals which do not carry a high load of recessive deleterious al-

leles, and which may already have a low level of heterozygosity (Leberg 1990). This strategy does not require a large number of founders. Such individuals may come from breeding programmes of captive animals, or from naturally inbred populations. In such new populations, homozygosity should not be a serious problem, but there would be a lower diversity of alleles. This condition may create an obstacle to future survival of the population if it is faced with new selective pressures. However, if the habitat of the species in question is a part of the landscape created by man, it will be less dependent on a capability to respond to a changing environment. Obviously, this strategy is more suited for populations that are created for economic reasons, such as provision of hunting opportunities, rather than for conservation purposes.

As indicated earlier, predictions of genetic theory about the success of small populations are, however, not supported unequivocally by evidence from the wild (Caughley 1994). Today, we know too little about in which taxonomic groups a certain amount of genetic variability really is crucial for the long-term survival of populations.

Two major points could be raised against the first strategy. The first one is the risk of outbreeding depression, so far a little studied phenomenon (Pusey & Wolf 1996). The second one is that one might wrongly refrain from attempting a reintroduction on the grounds that there is not sufficient genetic variation in the group available for introduction.

The second strategy is more straightforward, aiming at the creation of populations that can be utilised for economic or other reasons. This may of course be controversial for other reasons, e.g. the risk of hybridisation with native species or of unwanted ecological effects.

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