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PERSPECTIVES IN ORNITHOLOGY

INTRODUCED BIRDS AS MODEL SYSTEMS FOR THE CONSERVATION OF ENDANGERED NATIVE BIRDS

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A SMALL PASSERINE found only on the South Island of New Zealand, the Yellowhead (*Mohoua ochrocephala*) was once abundant and occurred in mature forests throughout its range (Gaze 1985). No estimates are available on the original population size, but based on the area of forest once available and recorded densities (Higgins and Peter 2002), there may have been 1–3 million Yellowheads when Europeans first reached New Zealand. Forest destruction and the introduction of exotic mammalian predators (against which the birds have little defense) have now reduced the species to less than 25% of its former range and a total population of less than a few thousand birds (Higgins and Peter 2002). Control of introduced predators in some populations on the mainland has been successful in reversing the decline, but this strategy is risky: the last surviving population of 15 birds in the north of the South Island increased to 99 birds after a decade-long program of predator control, only to disappear during a rat plague over a single winter (Higgins and Peter 2002).

The safest solution to ensure the survival of Yellowheads in the short term is to transfer birds to predator-free offshore islands, a strategy that has saved other New Zealand endemics from extinction (Armstrong and McLean 1995). For example, 27 Yellowheads were trapped on the mainland in 2001 and released on predator-free Ulva Island (Oppel and Beaven 2004). Although most Yellowhead translocations have succeeded thus far, it is not yet clear whether a few island populations will be enough to ensure the survival of this species if catastrophe should strike the remaining mainland birds. Should more island populations be created, using additional founders and salvaging the genetic variation present on the mainland before it disappears? Island translocations are expensive, and the Yellowhead must compete with other endangered species for a limited conservation budget (and space on islands). How many Yellowheads will be enough to ensure adequate genetic variation and their long-term survival? The question is neither trivial nor something to be debated only among academics. Conservation managers in the field need scientific guidelines to follow, and government must be convinced to fund agencies to support such guidelines.

The decline of a population to a low number and its subsequent recovery is termed a "population bottleneck." Although one might view the process as similar to wine passing through the neck of a bottle, the analogy can be misleading. The composition of wine does not change substantially between the wine bottle (pre-bottleneck) and the wine glass (post-bottleneck). Nor does the neck width of a wine bottle vary greatly among different vintages, whereas the size of a population bottleneck can

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vary from a single pair (in sexually reproducing organisms) to thousands of individuals. In the case of the Yellowhead, the bottleneck size on Ulva Island was 27 birds, a number typically used by conservation managers to found new populations of threatened birds (Griffith et al. 1989, Armstrong and McLean 1995, Wolf et al. 1996). Other species of endangered birds have been through even more severe bottlenecks. For example, the Black Robin (*Petroica traversi*) of the Chatham Islands declined to only five birds through the spread of exotic predators (Butler and Merton 1992). Similarly, the Mauritius Kestrel (*Falco punctatus*) survived as only a single breeding pair after its population collapsed from pesticide use and persecution (Jones et al. 1994). Such severe bottlenecks have not prevented at least some species from recovering; both the Black Robin and Mauritius Kestrel have now increased to several hundred birds (Butler and Merton 1992, Jones et al. 1994).

The recovery of some populations from a few surviving individuals might suggest that the consequences of bottlenecks may not be detrimental (and thus, 27 Yellowheads will be more than adequate). However, this is not the case, and one common consequence of severe bottlenecks is the loss of genetic diversity (Nei et al. 1975). A number of endangered species have low levels of genetic diversity as measured by levels of heterozygosity, allelic diversity per locus, and number of polymorphic loci. For example, the Black Robin has low levels of genetic diversity compared with other species (Ardern and Lambert 1997). Similar low levels of genetic diversity have been observed in other endangered birds, such as the Kakapo (*Strigops habroptilus*; Robertson 2006), though the endangered Guam Rail (*Rallus owstoni*) has retained levels of genetic variation comparable to other non-endangered rails (Haig and Ballou 1995). Severe bottlenecks generally lead to a loss of genetic diversity, because small populations are more subject to genetic drift, founder effects, and increased probabilities of inbreeding (Frankham et al. 2002).

The loss of genetic diversity in endangered species seems most pronounced in the species that have passed through the most severe bottlenecks (e.g., Ardern and Lambert 1997, Robertson 2006). However, quantifying the magnitude of genetic impoverishment in endangered species is difficult, because measures of genetic diversity from before the bottleneck event are seldom available. Using DNA extracted from historical study-skin specimens can provide pre-bottleneck samples, as long as enough birds are available and the skins originate from the same general location of the post-bottleneck population. Bouzat et al. (1998) used this technique to demonstrate that Greater Prairie-Chickens (*Tympanuchus cupido*) in Illinois lacked a number of alleles present in the pre-bottlenecked population. Similar "ghost" alleles were found in Mauritius Kestrels (Groombridge et al. 2000) using analyses of DNA from museum skin samples collected before the population's bottleneck. Isolated and bottlenecked populations of more common species have also been used to demonstrate the loss of genetic variation. For example, genetic variation was reduced in island populations of the New Zealand Robin (*P. australis*) that passed through severe bottlenecks, compared with populations of the same species on the mainland (Ardern and Lambert 1997).

The loss of genetic diversity in populations passing through small bottlenecks is likely to have negative fitness consequences, especially if the probability of inbreeding (mating of close relatives) increases in species passing through severe bottlenecks. Mating between relatives in severely bottlenecked populations may increase as a result of limited alternative options (e.g., all Black Robins are now descended from a single female; Butler and Merton 1992), and this can increase the probability of rare deleterious alleles being expressed. For example, increased incidences of abnormal or poorly performing sperm have been observed in Asiatic lions (*Panthera leo persica*) that passed through a bottleneck of less than 20 animals (Wildt et al. 1987). High levels of sperm abnormalities have also been found in inbred European rabbits (*Oryctolagus cuniculus*; Gage et al. 2006) and Cuvier's gazelles (*Gazella cuvieri*; Roldan et al. 1998). A wide range of studies on wild animals confirm that inbreeding can have negative effects on hatching success (Kempenaers et al. 1996), offspring survival, and recruitment (Brown and Brown 1998), mating success (Joron and Brakefield 2003), developmental symmetry (Lens et al. 2002), and susceptibility to disease (Reid et al. 2003). As a consequence, populations with high levels of inbreeding are likely to have an elevated risk of extinction (Saccheri et al. 1998,

Spielman et al. 2004, O'Grady et al. 2006). Even if such a population survives, the low levels of genetic diversity present may limit its ability to cope with future environmental changes (Frankham et al. 1999). Although it has been suggested that bottlenecks might sometimes be advantageous in purging deleterious alleles from a population, the evidence for purging is contradictory, and even severe bottlenecks are unlikely to fully purge a population (Frankham et al. 2001, Crnokrak and Barrett 2002, Swindell and Bouzat 2006). By contrast, there is clear evidence that bottlenecks can reduce the fitness of individuals (e.g., Roldan et al. 1998, Briskie and Macintosh 2004).

Although work on endangered animals has identified the genetic and fitness consequences of bottlenecks, most studies lack data from non-bottlenecked control populations, and this limits our ability to quantify the magnitude of bottleneck effects and the outcome in relation to bottleneck size. This makes it difficult to assess the consequences of different-sized bottlenecks for conservation purposes, and to set minimum population guidelines for conservation managers on the basis of controlled studies. The lack of non-bottlenecked control populations in studies of endangered species is often unavoidable, because most endangered species survive only in small bottlenecked populations. Nonetheless, in some endangered species, there are opportunities to control bottleneck effects by comparing among different populations that survive in different-sized bottlenecks (Wildt et al. 1987, Lens et al. 2002, Hale and Briskie 2006) or to use closely related common species as controls (Brock and White 1992, Haig and Ballou 1995). Isolated populations of abundant species have also been useful models for understanding the consequences of bottlenecks (Bensch et al. 1994, Keller et al. 1994, Keller 1998). However, there is a further group of animals that could provide a valuable model system for the study of bottlenecks—the many bird species that have been introduced to areas outside their range.

Introduced Species as Models for Bottlenecks

Birds have been transported and released into new areas by humans for centuries, but it was during the period of European expansion in the 19th century that bird introductions reached their peak (Long 1981). For example, during the late 19th century, more than 133 species of birds were introduced to New Zealand by a number of "acclimitisation societies," each importing plants and animals perceived as desirable for the new colonies (Thomson 1922, Long 1981). Today, about 30 species of exotic birds survive, and visitors to the settled parts of New Zealand are more likely to be greeted by a Blackbird (*Turdus merula*) or a Yellowhammer (*Emberiza citrinella*) than a native bird. Although some species were introduced for utilitarian purposes, such as hunting (e.g., Mallard [*Anas platyrhynchos*]) or predator control (e.g., Little Owl [*Athene noctua*]), most species were brought to New Zealand for sentimental or aesthetic purposes. Similar motives elsewhere have now led to a wide range of species established in populations far from their native ranges (Long 1981).

Introduced birds have a number of advantages over endangered birds for studying the genetic and fitness consequences of population bottlenecks. First, unlike endangered species, most introduced birds still have non-bottlenecked populations surviving in their native range, which can be used as non-bottlenecked controls. Thus, it is possible to study the fitness consequences of bottlenecks both "before" (the source population) and "after" (the introduced population) in ways not possible with endangered species that survive as only one or a few small post-bottlenecked populations (Briskie and Mackintosh 2004) or as a tray of bird skins in a museum collection. For many species, good records were kept of the numbers of birds released and, thus, of the size of the bottleneck each species passed through during its establishment (Thomson 1922). For example, the Greenfinch (*Carduelis chloris*) population in New Zealand was founded from about 70 birds, whereas Cirl Buntings (*E. cirlus*) became established on the South Island with less than 10 individuals released (Thomson 1922). This means that it may be possible to correlate founder number with fitness consequences in ways that can identify minimum bottleneck sizes below which the loss of fitness is deemed too high. Because many introductions (at least in New Zealand) occurred more than 130 years ago, introduced species also provide a chance to glimpse what happens to a bottlenecked population 50 to 100 generations after the event. This may be particularly useful for understanding what will happen to endangered species today

if they survive into the 22nd century. For some species, introductions occurred in a number of different locations. Thus, European Starlings (*Sturnus vulgaris*) were introduced not only to North America, but also independently to New Zealand, Australia, South Africa, and Fiji. This provides the opportunity to include replicates in a study of bottleneck effects and, because the sizes of the founding populations for each locality are usually different, to assess the effect of bottleneck size on fitness. Finally, introduced species provide options for more invasive and destructive sampling that are not possible with endangered species. For example, to determine whether increased hatching failure in an endangered species is attributable to infertility, a census of sperm numbers on the perivitelline membranes of freshly laid eggs can be used to determine whether sperm failed to reach the egg (Birkhead et al. 1994, Wishart 2002). However, because the method requires the destruction of eggs, it is unlikely to be justified in highly endangered birds. Instead, introduced species can provide a model system for understanding problems in fertility of bottlenecked populations without harming an endangered species.

Despite these advantages, introduced species have some drawbacks. First, it is unclear whether introduced species that can tolerate a wide range of habitats and environmental conditions, such as the House Sparrow (*Passer domesticus*), are a suitable model for a specialized endangered species with a narrow ecological niche. In other words, each species (introduced or native) is likely to have unique characteristics that limit the value of extrapolating from other species. The number of founders for some introduced species is also not known, or it is unclear if the estimates are accurate (Long 1981). Whereas New Zealand's acclimitisation societies left good records of the numbers of birds they purchased and ultimately released (Thomson 1922), introductions elsewhere were often done by private individuals, who left fewer records. Species that are popular as pets, such as parrots and finches, may also be particularly unsuitable for the study of bottlenecks, because feral populations are likely to be continually supplemented from additional escapes. Although one of the main advantages of introduced species as a model for studying bottlenecks is the availability of a control population in their native range, this may not be the case if the source populations have also declined. For example, Song Thrushes (*T. philomelos*) are among the most abundant birds in New Zealand, but they have declined dramatically in their source population in Great Britain (Robinson et al. 2004). Similarly, Cirl Buntings have a restricted range and are considered uncommon in New Zealand (2,000–5,000 individuals; Heather and Robertson 1996), but they have declined to only a few hundred in their source population in southern England (Wotton et al. 2000). Finally, environmental differences between the source and introduced ranges may obscure the effects of bottlenecks and limit their usefulness for saving endangered species within their own environment. In practice, introduced species are more likely to become established when the abiotic conditions are similar to those of their native range (Blackburn and Duncan 2001), but some differences in environmental conditions between native and introduced ranges might even be advantageous in studying how bottlenecks affect the ability of a population to cope with such changes. Perhaps the New Zealand population of Blackbirds sourced from the cold and damp climate of Britain, which now find themselves in a warmer and drier climate, will give us some insight into how the source populations will fare in an era of global warming.

Geneticists have long recognized the value of introduced species for understanding the genetic consequences of population bottlenecks. For example, Baker and Moeed (1987) compared Common Mynas (*Acridotheres tristis*) that had been introduced to Australia, New Zealand, Fiji, Hawaii, and South Africa and found that these populations typically had lower heterozygosity, fewer alleles per locus, and lower percentages of polymorphic loci than the source population in India. The South African population of Common Mynas went through the most severe bottleneck during its establishment and, as expected, showed the greatest reduction in genetic diversity (Baker and Moeed 1987). Introduced populations of House Sparrows, European Starlings, Greenfinches, and Eurasian Tree Sparrows (*P. montanus*) likewise have reduced genetic variation compared with their source populations, though how much they differ varies across species and populations (Ross 1983, Parkin and Cole 1985, St. Louis and Barlow 1988, Cabe 1998). In a review of previous studies of introduced populations, Merilä et al. (1996)

confirmed the prediction that reductions in levels of genetic variation were inversely proportional to the size of the founder population. In other words, populations of introduced species founded by fewer individuals and, thus, having passed through a severe bottleneck during their establishment, appear to lose more genetic variation, on average, than species passing through less severe bottlenecks. Although the number of introduced species in this analysis was small, the relationship between bottleneck size and genetic diversity appears to be linear, and it is only at bottleneck sizes between 300 and 400 individuals that levels of heterozygosity and percentage of polymorphic loci no longer differ between source and introduced populations (Merilä et al. 1996). Such bottlenecks are much larger than that used to found new populations of endangered birds in New Zealand, such as the Yellowhead, but some caution is necessary, given that this value is based on a very small data set, and further studies need to be done.

The phenotypic consequences to individuals and populations of introduced species passing through a bottleneck have also attracted the attention of evolutionary biologists and deserve further work by conservation biologists. For example, one of the best examples of rapid morphological changes in a post-bottlenecked population is that of introduced House Sparrows in North America (Johnston and Selander 1971). Changes in the size of North American House Sparrows correlates with climatic differences they encounter across their introduced range, which suggests rapid development of adaptations to local environments. A comparison of Eurasian Tree Sparrow morphology likewise found significant changes in body size, tail length, and bill size of birds in an introduced population in the St. Louis area, Missouri, compared with their source population in Germany (Barlow 1980, St. Louis and Barlow 1991). The Eurasian Tree Sparrow passed through a relatively severe bottleneck during its establishment (20 birds), and it has been suggested that the loss of genetic variation it incurred might also reduce variance in morphological structure (Mayr 1954). However, the North American population of Eurasian Tree Sparrows did not show any reduced variation in a variety of skeletal measures, which suggests no concomitant loss of variation in structure with genetic variation (St. Louis and Barlow 1991). Whether other populations of severely bottlenecked birds retain levels of phenotypic variation similar to those of their source populations could readily be examined in a variety of other species. Such comparisons are not as easy with endangered species passing through bottlenecks, because of the problems associated with obtaining pre-bottleneck data, but can readily be done using introduced species as a surrogate model. Future work on morphological changes in introduced species could also examine patterns of developmental abnormalities, given that inbreeding and small bottlenecks have been found to increase levels of fluctuating asymmetry in some species (Roldan et al. 1998, Lens et al. 2002).

Because inbreeding generally reduces reproductive success in birds, it could lead to lower reproductive success and decreased growth rates for populations of endangered species passing through severe bottlenecks. It is interesting to note that both clutch size and egg size have declined among introduced species in New Zealand (Cassey et al. 2005, Evans et al. 2005), but whether this is attributable to life-history adaptations to the introduced environment or related to the effects of bottlenecks they passed through during their establishment is not clear. In a comparative study of 22 native New Zealand species that had passed through various bottleneck sizes, hatching failure increased dramatically with severity of bottleneck size (Briskie and Mackintosh 2004). Those species passing through bottlenecks of less than 150 individuals had much higher rates of hatching failure than species with more than 150 birds. No data from pre-bottlenecked populations of these endangered native species were available to act as controls, but the same analysis, comparing 15 introduced species in New Zealand with their source populations, confirmed that hatching failure increased with severity of bottleneck size, especially in bottlenecks of fewer than 150 founders. Interestingly, differences in rates of hatching failure between introduced New Zealand birds and their source populations disappeared entirely only when the number of founders was close to 600 individuals (Briskie and Mackintosh 2004). Such bottleneck sizes fall within the range of the 50/500 rule suggested by Franklin (1980) for the short- and long-term survival of populations, respectively, but above the range generally used by conservation biologists when founding new

populations of endangered species (Griffith et al. 1989, Armstrong and McLean 1995). If the pattern found in introduced New Zealand birds turns out to be a general phenomenon, conservation biologists may be underestimating the effects of bottlenecks on fitness traits associated with reproduction. Additional analyses of other introduced species would be valuable to confirm and fine-tune these estimates, but it is clear that more focused studies of the reproductive biology of introduced species can contribute to a better understanding of bottleneck effects in endangered native species.

The role of disease (and especially emerging diseases) in avian population dynamics is currently attracting widespread attention (Friend et al. 2001). Decreased genetic diversity, including decreased MHC allele diversity in endangered species (Miller and Lambert 2004, Spielman et al. 2004), raises the possibility of increased catastrophic loss of bottlenecked populations to disease. Conservation of endangered species may thus increasingly depend on understanding the dynamics of diseases and other pathogens in bottlenecked populations. On the one hand, severe bottlenecks are expected to reduce the diversity of pathogens in a post-bottlenecked population, given that a small number of individuals during a bottleneck will be unable to support viable populations of at least some pathogens. Studies of introduced species in both their source and introduced ranges confirm that introduced species have fewer parasites (Torchin et al. 2003). An examination of haematozoan parasites in Common Myna populations likewise found reduced infection levels in two introduced populations on oceanic islands (Fiji and Hawaii), but not in six other introduced populations (Ishtiaq et al. 2006). On the other hand, the loss of genetic diversity associated with bottlenecks may make a post-bottlenecked population more susceptible to epidemics. For example, eastern North American populations of the House Finch (*Carpodacus mexicanus*) were founded by introductions in the 1940s and resulted in a loss of genetic diversity in the current population (Hawley et al. 2006). The rapid spread of a *Mycoplasma* epidemic in eastern House Finches has been attributed to their compromised immune system following the earlier bottleneck (Hawley et al. 2005).

Despite the potential importance of disease threats to endangered birds, experimental work on the immune system of introduced birds that have passed through severe bottlenecks is limited. Lee et al. (2005) recently compared the immune responses of introduced House Sparrows and Eurasian Tree Sparrows in North America and found that the latter incurred a much higher fitness cost when experimentally challenged with killed-bacteria injections. Given that Eurasian Tree Sparrows went through a more severe bottleneck (about 20 individuals) than House Sparrows (about 100 individuals), this result is consistent with increased deleterious effects of bottlenecks on immune-system function. However, Lee et al. (2005) did not compare the immune responses of these species in their introduced populations with those in their native ranges. Such studies are now needed to determine how immunocompetence varies with bottleneck size and whether endangered species are more vulnerable than previously supposed. As with other fitness traits, the ability to test introduced species in both their native and introduced ranges provides a chance to quantify the deleterious effects of bottlenecks on immune-system function and to relate these effects to founder number.

The Value of Introduced Species

Introduced birds generally have a poor standing among both bird watchers and ornithologists. Perhaps like many other researchers, I viewed House Sparrows, European Starlings, and other introduced birds as "trash," whose only conservation value lay in visibly reminding people of the folly of transplanting animals where they do not belong. Even when introduced species are grudgingly accepted as part of the modern avifauna, they still retain a stigma of somehow being less interesting than native species. I now believe this view is wrong, and such species can provide a valuable model system for studying native birds now facing a bottleneck crisis of their own. Introduced species provide the opportunity to conduct a multitude of studies on the consequences of severe population bottlenecks, but without jeopardizing native birds in the process. This does not diminish or replace the need to study endangered birds; no doubt each species has slight differences and unique traits that make it risky to extrapolate indiscriminantly from abundant introduced species to declining native species. Indeed, small

and declining populations of introduced species such as the Sky Lark (*Alauda arvensis*) in British Columbia might even be useful models for understanding the processes of decline in small populations of native species. Although catching a glimpse of the endangered Yellowhead in a New Zealand forest will no doubt continue to excite me more than seeing an introduced Yellowhammer in a nearby clear-cut, there is much value in studying how both species are coping with the bottlenecks each has faced.

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