

10. General conclusions

There is now convincing evidence that many of our threatened avian endemics have lost considerable genetic variation since the arrival of humans and their associated introduced pests and predators. The most vulnerable endemics are already extinct, and extant threatened species only survive in small numbers in isolated mainland habitats or on offshore islands and generally possess low levels of genetic diversity. The eradication and control of introduced predators, particularly on many offshore islands, has enabled populations of highly threatened species to recover in numbers and thus reduced their immediate extinction risk, although many species confined to the mainland continue to show worrying signs of population decline. As long as populations are in decline due to extrinsic pressures such as introduced predators, intrinsic factors such as genetic diversity and inbreeding depression are of little consequence because their impacts on population fitness are much more gradual. Perhaps counter-intuitively, the greatest impact of genetic factors will be found in small populations that have stabilised or are growing slowly due to management. Because mutation rates (which ultimately generate new genetic variation) are relatively slow, genetically depauperate species continue to be at risk due to reduced immune capabilities associated with genetic homogeneity as well as the reduced ability to genetically adapt to changing environmental pressure through the process of natural selection.

The potential for further and immediate losses of genetic variation during founder events of translocated populations is also a potential problem. However, studies have so far indicated that founder events are not as important (as long as reasonable numbers of individuals are transferred and released) as the subsequent increase in the rate of inbreeding and genetic drift associated with small, finite population sizes of island sites. Conservation biologists worry particularly about inbreeding because it not only leads to reduced genetic diversity (and hence reduced adaptiveness and increased vulnerability) but it also reduces individual fitness, mostly as a consequence of the increased probability of expressing deleterious recessive alleles. To what extent reduced individual fitness translates into reduced population fitness and growth rates will depend on the frequency of close inbreeding, the overall rate of inbreeding, the magnitude of inbreeding depression and which life history traits are affected. For example, an effect on early life history traits such as depressed hatching rates may not be as detrimental as effects on later life history traits such as lower juvenile recruitment rates, although it is likely that loss of fitness due to inbreeding depression will accumulate across life history stages (Szulkin et al. 2007).

11. Recommendations

The following recommendations have arisen from this research programme:

- Guidelines for translocations should be updated to include information that ensures potential issues surrounding genetic diversity and inbreeding are flagged and addressed. (See section 1.)
- Given that a number of studies have failed to detect adverse effects of taking a small quantity of blood from birds (if done properly), and that blood has several advantages over feathers (although the latter is preferred over not taking any samples), it is recommended that proposals for translocations include a section to justify why samples for DNA analysis are *not* required (e.g. 'Recovery group indicated samples were collected during two previous translocations and further samples are not required'). Otherwise, details for collecting a small (<0.1 mL) quantity of blood from *each* individual (rather than minimum numbers) should be specified, and potential research questions and outcomes outlined, even if a science provider to carry out the analysis has not yet been identified. (See section 3.)
- Given that mainland populations tend to retain greater genetic diversity than island populations, resources for predator control on mainland sites (rather than exclusively for island populations) should be maintained or increased to retain this important source of genetic diversity. (See section 6.)
- Maintaining genetic diversity in small island populations for relatively low-density species such as takahe will be extremely difficult without management intervention. Releasing one (reproducing) individual per generation may circumvent most effects of population isolation, while minimising the stress and expense associated with translocation. However, unless a population is exhibiting severe inbreeding depression or is on the verge of extinction, mixing subspecies or strongly divergent populations (i.e. those that have been separated for thousands of years) should be avoided. (See section 6.)
- Both ecological and genetic criteria need to be considered when assessing needs and impacts of translocation (currently in New Zealand only ecological concerns tend to be stressed). For example, when deciding on numbers of individuals and from where to source them, there should be justifications that the translocation is unlikely to result in significant loss of genetic diversity or genetic representation. Any translocation that would result in a serial bottleneck of a threatened species, or would involve mixing of subspecies or historically divergent populations, should require clear and strong justification. Finally, translocations that are carried out solely for the purpose of potentially increasing genetic diversity and/or population fitness should be considered experimental at this stage and should be designed with care. (See section 6.)
- For translocations and reintroductions, consideration should be given to the minimum number of individuals that should be released, rather than just focussing on the minimum number of individuals needed to establish a breeding population, to limit the loss of genetic variation due to drift and minimise the probability of close inbreeding while the population is still small. Although formal modelling has yet to be carried out, studies of SI saddlebacks

and mohua that are currently in progress suggest that island populations should be established with a minimum of 15–30 pairs (30–60 individuals), respectively (see section 6). For intensively managed species such as takahe, kakapo and kokako, further precautions over founder representation are advised to prevent a disproportionate number of the descendants coming from relatively few successful pairs/females (see section 7).

- The rate at which the mean level of inbreeding increases in a closed population is primarily dependent on the carrying capacity of the site. For species with low population densities, it is strongly urged that recovery groups assess the potential carrying capacity of relatively small sites and estimate the likelihood of requiring future translocations to prevent high levels of inbreeding being reached. As a general rule, an outbred population with a stable population size of ten individuals (= five breeding pairs) will become inbred at $F > 0.25$ (brother–sister relatedness) in six generations; this level will be reached more quickly if the population size fluctuates or if individuals are harvested for translocation. Note that recruitment rates of newly translocated immigrants will be relatively low at the population's carrying capacity, making the management goal of reducing the level of inbreeding even more difficult to achieve. Even islands or fenced reserves containing populations with relatively high numbers (e.g. 100–200 individuals) will require some form of management (e.g. introducing new genetic stock) to reduce the level of inbreeding. (See section 7.)
- Although current studies did not examine the relationship between inbreeding depression and lowered population viability, it would be unwise to ignore a considerable volume of theory and other evidence that shows such a link. Future modelling efforts will provide a clearer picture of the effects of inbreeding on population fitness, and indicate how long managers have before they may need to act. It needs to be stressed that the negative consequences of inbreeding depression on growth rates of populations established on predator-free sites will occur only after many generations of inbreeding—while the risk of reinvasion by rats and stoats to the same islands is a day-to-day threat. Nevertheless, assuming that predator reinvasions can be managed and their risk to the population minimised, it is recommended that managers attempt, where practical, to also minimise the build-up of high levels of inbreeding. (See section 8.)
- There is increasing evidence of a link between loss of genetic diversity and increased susceptibility to disease. The generally low levels of genetic diversity found in many of our endemics is a reminder of their vulnerability to diseases and of the need to try to minimise further losses, especially for more genetically diverse species. The best way to prevent further losses is to avoid prolonged population bottlenecks and maintain gene flow across recently isolated populations, through translocation if necessary. However, it needs to be recognised that very little can be achieved through direct management in single-population species that have already lost significant genetic variation, except of course to minimise the risks of introducing disease. (See section 9.)

These recommendations should not be seen as conclusive or in isolation from other factors, but rather as new data and evidence to be considered alongside a host of other data, evidence and policy used to inform management decisions. Many of the results of this research remain inconclusive partly because of the nature of studying processes that work across generation times rather than years. Inevitably, there is a call for more research and more funding to understand further what everyone agrees are complicated processes.

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Appendix 1

DEFINITIONS AND CONCEPTS

There are two main fitness consequences of small population sizes that are important to distinguish throughout this paper:

1. **Loss of genetic diversity:** This is caused by stochastic processes such as genetic drift (random loss of alleles due to mortality or failed breeding) and founder effects (random loss of alleles during founder events), which are much more likely to occur when populations have gone through a bottleneck event (see below). Inbreeding can also cause loss of genetic variation in that it results in decreased heterozygosity and increased homozygosity.
2. **Inbreeding depression:** This is where inbreeding leads to a reduction in individual fitness through an increase in homozygosity across genomes, which results in either the loss of heterozygous advantage or the increased expression of homozygous recessive alleles, which are often harmful and lead to an immediate reduction in fitness of the related parents.

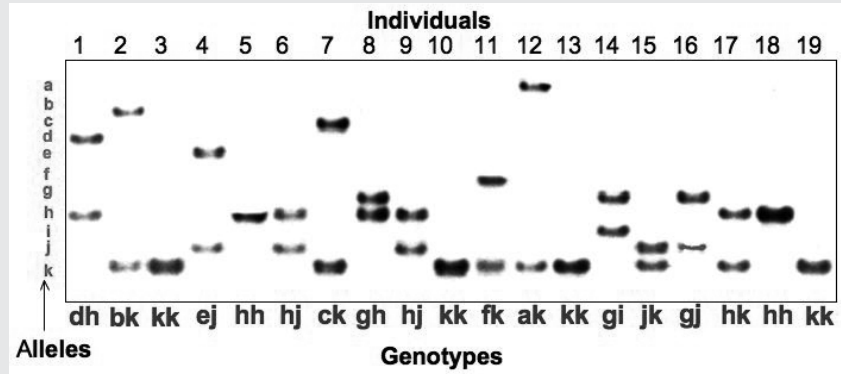
How does a population bottleneck result in genetic bottleneck? When a population experiences a bottleneck event (such as loss of habitat, predator outbreak or a translocation), the surviving population is small relative to the original population. As a simple consequence of the small sample size and chance, rare alleles tend to be lost and not represented in the surviving population, and common alleles can be over/under-represented relative to their proportion in the original population. Loss of genetic variation during founder events associated with translocation can occur at the point of initial capture, or as a result of poor survival of released birds or differential breeding success of released pairs.

It is worth noting that the small surviving population is also likely to be subject to inbreeding. Inbreeding does not result in loss of alleles but leads to a decrease in heterozygosity and an increase in homozygosity of alleles, which is a form of loss of genetic variation (see Box 1). The long-term consequence of loss of genetic diversity is a reduced evolutionary responsiveness, which can lead to a reduced ability of a population to adapt to changes in the environment such as new pathogens/diseases or long-term climate change. Note that the consequences of loss of genetic variation tend to be long-term and the impact depends on how much the environment changes; i.e. loss of genetic diversity might have no immediate negative consequences as long as the environment the animals are living in remains more or less constant.

It is sometimes worth distinguishing between 'within population' inbreeding, which is mating between relatives, and 'between population' inbreeding, where one population is more inbred than another and thus has lower fitness (Keller & Waller 2002). Inbreeding can result in mutants or ill-formed offspring, but in wild populations these will often die and therefore be less likely to be detected. It can be helpful to think of inbreeding as resulting in increased susceptibility to environmentally inflicted mortality. Indeed, recent research suggests that inbreeding depression may be difficult to detect in benign environments where inbred individuals can have similar fitness to outbred individuals (Keller & Waller 2002). In other words, inbreeding depression is often environmentally sensitive.

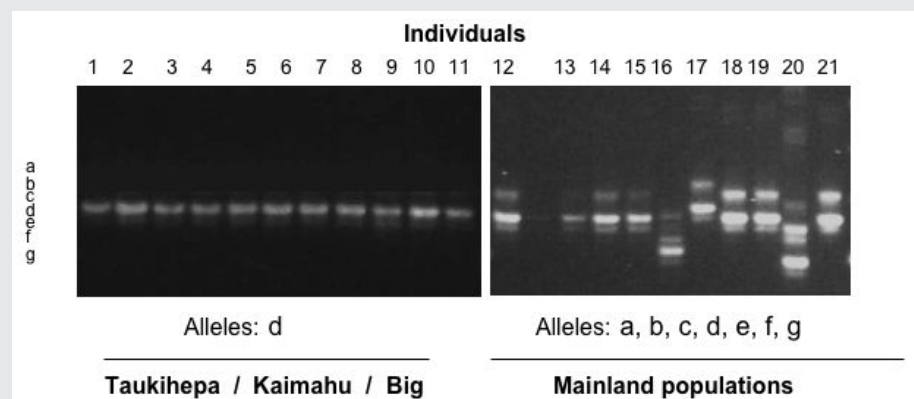
Box 1. What is meant by genetic diversity?

The diagram below illustrates the two main metrics used to quantify genetic diversity—allelic diversity, which describes the number of alleles present at a given genetic locus, and observed heterozygosity (*H*), which is the proportion of individuals in a population that are heterozygous at a particular locus.



Each **locus** (a section of a chromosome) of an individual consists of two **alleles** (one copy each from the mother and father), and these in combination form a **genotype**. Alleles (a–k) separate out on the gel according to their weight. In the example shown for one locus sampled across 19 individuals (all from the same population), there are 11 different alleles and 14 different genotypes, for which 13 of 19 individuals (68%) are **heterozygous** (have two different alleles) and the remaining 6 (32%) are **homozygous** (have two copies of the same allele, and hence appear darker on the gel). This locus would be considered to show a high level of genetic diversity because of the relatively large number of different alleles in the population and the large proportion of heterozygotes. After amplifying a number of different loci in the 19 individuals, the number of alleles per locus and the proportion of heterozygotes averaged across loci can be calculated to estimate the genetic diversity of the population.

The diagram below shows one microsatellite DNA locus of the South Island saddleback (*Philesturnus carunculatus carunculatus*), and illustrates that genetic diversity was extremely low in the remnant population on Taukihepa (Big South Cape Island) and in the contemporary populations on Kaimahu and Big Islands relative to historic populations on the mainland.



When managers are uncertain about whether to source individuals for translocations from a single (possibly bottlenecked) population or from two or more separate populations, they are normally concerned about genetic variation and giving the reintroduced population its best chance at long-term survival. On the other hand, when managers try to boost the population growth rate of a small isolated population on a predator-free island (which may be experiencing lower than normal fertility rates or low juvenile recruitment) by introducing new breeding stock from a more genetically diverse population, they are concerned about the effects of inbreeding depression. Although both loss of genetic diversity and inbreeding depression have important implications for conserving populations, there is a tendency for the maintenance of genetic variation during reintroductions to take a lower priority because the beneficial effects are often insidious and take a long time to manifest—normally outside the timeframes of standard recovery programme planning.

Genetic diversity is measured using molecular markers such as microsatellites and is estimated in two ways:

1. The average number of alleles per locus (which when weighted by differences in sample sizes between populations is referred to as *allelic richness*)
2. The proportion of alleles that are heterozygous (*H*) (see Box 1)

Inbreeding is best measured through the use of pedigrees, as the use of molecular markers to estimate levels of heterozygosity and hence infer the level of inbreeding is less accurate and controversial (Grueber et al. 2008b). When derived from pedigrees, inbreeding is estimated in terms of inbreeding coefficients (*F*), which represent the probability that two alleles will be identical (homozygous) due to inheritance through a common ancestor. It is important to note that individuals can attain homozygous alleles due to chance, but that this probability increases with increasing levels of relatedness between the mother and the father. The highest level of inbreeding in any one generation is $F=0.50$, for organisms that are able to self (e.g. plants) and 0.25 for organisms that reproduce sexually (see Table A1.1). However, inbreeding can accumulate across generations; if the offspring from a full-sib pairing also paired and bred, then their offspring would have an $F=0.375$. Furthermore, in very small, closed populations, inbreeding is unavoidable because eventually all individuals become closely related, even if they avoided mating with their closest kin. For example, if we assume that a breeding population is fixed at two pairs and each pair has a male and female offspring, even if these offspring outbreed each generation, average *F* increases

so that after just four generations all breeders are related to each other at $F=0.25$. Researchers tend to distinguish between an increase in the mean level of inbreeding due to mating between close relatives and that due to the background level of inbreeding.

Technically, only individuals can have inbreeding coefficients, while breeding pairs share kinship coefficients, which is equivalent to the inbreeding coefficient of the pair's offspring. Nevertheless, many studies will refer to a pair's inbreeding coefficient when expressing the degree of relatedness between a mother and father.

TABLE A1.1. COEFFICIENT OF INBREEDING (*F*) FOR ANY OFFSPRING PRODUCED FROM MATINGS BETWEEN VARIOUS KINDS OF RELATIVES.

| TYPE OF MATING | <i>F</i> |
|--|---------------|
| Selfing | ½ (0.50) |
| Full-sibs | ¼ (0.25) |
| Uncle × niece; aunt × nephew; double cousins | ⅛ (0.125) |
| First cousins | ⅙ (0.0625) |
| First cousins once removed | ⅓₂ (0.03125) |
| Second cousins | ⅙₄ (0.0156) |
| Second cousins once removed | ⅙₁₂₈ (0.0078) |

Do New Zealand threatened birds have low genetic diversity and high levels of inbreeding?

Many New Zealand threatened bird species persist in small and isolated populations. Research indicates that temporary bottlenecks associated with translocations contribute less to the loss of genetic variation than the small sizes of island populations. Inbreeding within these island populations can result in further reductions in individual fitness. There is evidence of moderate inbreeding depression in North Island robins on Tiritiri Matangi and weak inbreeding depression in takahē translocated to offshore islands. The maintenance of genetic diversity should become a fundamental component of long-term management strategies for threatened species in New Zealand.

Jamieson, I.G. 2009: Loss of genetic diversity and inbreeding in New Zealand's threatened bird species. *Science for Conservation* 293. 59 p.