



Founder Effects, Inbreeding, and Loss of Genetic Diversity in Four Avian Reintroduction Programs

IAN G. JAMIESON

Department of Zoology, University of Otago, P.O. Box 56, Dunedin, New Zealand, email ian.jamieson@stonebow.otago.ac.nz

Abstract: The number of individuals translocated and released as part of a reintroduction is often small, as is the final established population, because the reintroduction site is typically small. Small founder and small resulting populations can result in population bottlenecks, which are associated with increased rates of inbreeding and loss of genetic diversity, both of which can affect the long-term viability of reintroduced populations. I used information derived from pedigrees of four monogamous bird species reintroduced onto two different islands (220 and 259 ha) in New Zealand to compare the pattern of inbreeding and loss of genetic diversity among the reintroduced populations. Although reintroduced populations founded with few individuals had higher levels of inbreeding, as predicted, other factors, including biased sex ratio and skewed breeding success, contributed to high levels of inbreeding and loss of genetic diversity. Of the 10–58 individuals released, 4–25 genetic founders contributed at least one living descendent and yielded approximately 3–11 founder-genome equivalents (number of genetic founders assuming an equal contribution of offspring and no random loss of alleles across generations) after seven breeding seasons. This range is much lower than the 20 founder-genome equivalents recommended for captive-bred populations. Although the level of inbreeding in one reintroduced population initially reached three times that of a closely related species, the long-term estimated rate of inbreeding of this one population was approximately one-third that of the other species due to differences in carrying capacities of the respective reintroduction sites. The increasing number of reintroductions to suitable areas that are smaller than those I examined here suggests that it might be useful to develop long-term strategies and guidelines for reintroduction programs, which would minimize inbreeding and maintain genetic diversity.

Keywords: founder genome equivalents, founder size, genetic diversity, inbreeding, New Zealand, pedigrees, *Petroica australis rakiura*, *Petroica longipes*, *Philesturnus carunculatus carunculatus*, *Porphyrio hochstetteri*, reintroductions

Efecto Fundador, Endogamia y Pérdida de Diversidad Genética en Cuatro Programas de Reintroducción de Aves

Resumen: El número de individuos translocados y liberados como parte de una reintroducción a menudo es pequeño, como lo es la población establecida final, debido a que el sitio de reintroducción es típicamente pequeño. Poblaciones fundadoras y resultantes pequeñas pueden conducir a cuellos de botella, que son asociados con incrementos en las tasas de endogamia y la pérdida de diversidad genética, que pueden afectar la viabilidad a largo plazo de las poblaciones reintroducidas. Utilicé información derivada de los pedigrís de 4 especies de aves monógamas reintroducidas en dos islas diferentes (220 y 259 ha) en Nueva Zelanda para comparar el patrón de endogamia y de pérdida de diversidad genética entre las poblaciones reintroducidas. Aunque las poblaciones reintroducidas fundadas con pocos individuos tuvieron niveles altos de endogamia, como se esperaba, otros factores, incluyendo sesgos en la proporción de sexos y en el éxito reproductivo, contribuyeron a niveles altos de endogamia y pérdida de diversidad genética. De los 10–58 individuos liberados, 4–25 fundadores genéticos contribuyeron con por lo menos un descendiente vivo y produjeron 3–11 equivalentes de genoma fundador (número de fundadores genéticos asumiendo una contribución equivalente de descendientes y una pérdida no aleatoria de alelos a lo largo de varias generaciones) después

de siete temporadas de reproducción. Este rango es mucho menor que los 20 equivalentes de genoma fundador recomendados para poblaciones criadas en cautiverio. Aunque el nivel de endogamia en una población reintroducida inicialmente fue tres veces mayor que el de una especie relacionada cercanamente, la tasa de endogamia estimada a largo plazo en esta población fue aproximadamente la tercera parte de las otras especies debido a diferencias en las capacidades de carga de los sitios de reintroducción respectivos. El creciente número de reintroducciones en áreas adecuadas que son más pequeñas que las que examiné sugiere que puede ser útil desarrollar estrategias y directrices a largo plazo para los programas de reintroducción, con las que se puede minimizar la endogamia y mantener la diversidad genética.

Palabras Clave: diversidad genética, endogamia, equivalentes de genoma fundador, *Petroica australis rakiura*, *Petroica longipes*, *Philesturnus carunculatus carunculatus*, *Porphyrho hochstetteri*, Nueva Zelanda, reintroducciones, tamaño fundador

Introduction

Species reintroductions are becoming a more common element in conservation efforts (Armstrong & Seddon 2008) because in some cases species' habitats can be restored to nearly pristine conditions. For instance, advances in poison baits and their deployment has enabled eradication of non-native predators, such as rats, from offshore islands, which has made these sites feasible for reintroduction (Towns & Broome 2003). Similar improvements in predator-proof fencing (Speedy et al. 2007) have improved the status of protected areas on mainland, where high reinvasion rates of introduced predators makes poison and trapping operations impractical.

The number of individuals translocated to islands or released in fenced areas is often small, as is the resulting population, because the reintroduction sites are small or have limited carrying capacities. Small founder and resulting populations are associated with increased rates of inbreeding and loss of genetic diversity, both of which can reduce the long-term fitness of a population (Frankham et al. 2002). The genetic effects of the size of the founder and resulting population in island reintroductions are exacerbated by the fact that island sites are typically isolated from other populations, which prevents immigration and gene flow (i.e., many reintroduced island populations are effectively closed populations). Without gene flow, the mean level of inbreeding will increase over time leading to a loss of genetic diversity and population fitness (Frankham et al. 2002).

Breeding strategies for management of captive populations are designed to minimize inbreeding and loss of genetic variation (Lacy 1994), but these strategies have not been applied to the management of wild, free-ranging, reintroduced populations. One reason for the lack of studies in wild populations is that the pedigrees necessary for calculating inbreeding coefficients are not easily obtained from natural populations (Pemberton 2004). For the pedigree studies of wild populations that do exist, many are on birds and most of these have focused on island populations (Keller & Waller 2002). Nevertheless, few pedigree studies of wild populations have been on threatened species (Haig & Ballou 2002), and fewer

still have followed the extent of inbreeding since an island population was first established (e.g., Grueber & Jamieson 2008; Ewing et al. 2008).

I used pedigree data from four reintroduced populations on two islands to examine the effects of the size of the founder and resulting populations on the rate of inbreeding and associated loss of genetic diversity. The four threatened bird species were South Island Saddleback (*Philesturnus carunculatus carunculatus*), Stewart Island Robin (*Petroica australis rakiura*), North Island Robin (*Petroica longipes*), and Takahe (*Porphyrho hochstetteri*). These species are all socially (and genetically) monogamous and thus lend themselves to the construction of reliable pedigrees. The four reintroduced populations varied in their initial release or propagule sizes and the two island sites varied in their estimated carrying capacities.

Methods

Study Sites and Sampling

As with most species endemic to New Zealand, the four study species were once widespread and common throughout the mainland of North and South islands (robins and saddlebacks were also found on numerous coastal islands) before the arrival of humans and the associated introduction of mammalian predators, such as rats, mustelids, and feral cats (Innes et al. 2010). The study sites were on two island protected areas: Tiritiri Matangi (hereafter Tiritiri) and Ulva islands (Fig. 1), where several native species have been reintroduced following the eradication of introduced predators in 1993 and 1996, respectively (Armstrong & Ewen 2002; B. Beaven, unpublished data). Ulva Island (259 ha) is 800 m from the nearest shoreline in Stewart Island's Paterson Inlet, and Tiritiri (220 ha) is in the Hauraki Gulf, 3.5 km from the mainland (Fig. 1).

Takahe are flightless and have been extirpated from the mainland except in isolated mountains in Fiordland, South Island, but they have been translocated to several offshore islands, including Tiritiri. South Island

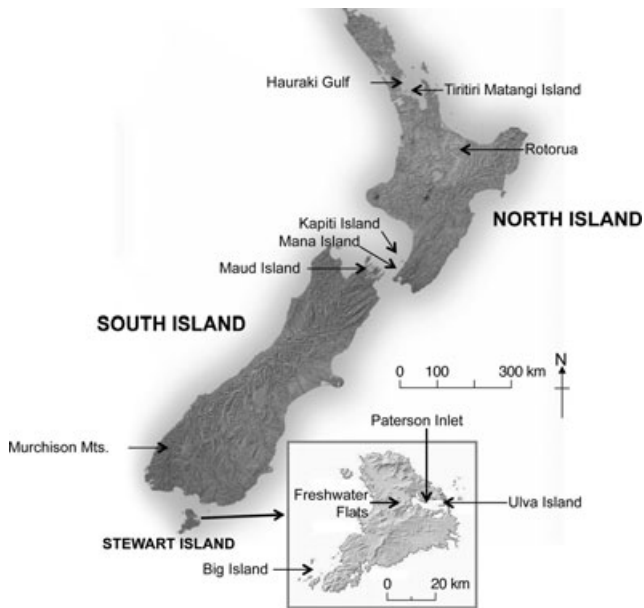


Figure 1. Map of North, South, and Stewart islands of New Zealand and sites where the four study species (Stewart Island Robin, South Island Saddleback, North Island Robin, and Takahe) originated and were reintroduced.

Saddlebacks have also been extirpated from the mainland, but the species have been reintroduced to numerous islands throughout the South Island. Saddlebacks are not capable of sustained flight and therefore are normally confined to individual offshore islands. The distribution of the robin species is patchy throughout New Zealand's mainland forests, but they have been reintroduced to many offshore islands. During the study period, there were no resident North Island Robin populations on the mainland adjacent to Tiritiri Island. The closest Stewart Island Robin population to Ulva Island was 25 km away, and there was no evidence of banded robins from the Stewart Island population immigrating to Ulva (B. Beaven, personal communication). On the basis of the above information, I considered the study populations closed systems.

Although translocation exposed birds to short-term stress, postrelease survival tended to be high in all four species, and the birds' breeding behavior after reintroductions was typical for their species (Armstrong 1995; Armstrong & Craig 1995; Jamieson & Wilson 2003). The study populations were free-ranging, and birds were not reliant on supplementary feeding. Both robin species tend to breed in their first year, saddlebacks in their second, and Takahe in their second or third years, and all four species form long-term pair bonds and exhibit bi-parental care (I.J., unpublished data). Observations of courtship feeding and incubation behaviors were used to determine the sex of saddlebacks and robins (Armstrong

2001; Hooson & Jamieson 2003), and DNA tests were used for sexing Takahe (Department of Conservation, unpublished data).

Reintroduction of Robins and Saddlebacks to Ulva Island

The interior, mature, podocarp forest of Ulva Island is surrounded by stunted coastal forest. Thirty color-banded South Island Saddlebacks (28 adults and 2 juveniles) were translocated in April 2000 from Big Island to Ulva Island (Fig. 1), of which 23 survived to the first breeding season (I.J., unpublished data). There was no extensive nest monitoring in the first breeding season, but six breeding pairs were identified from observations and subsequent parentage analysis and a further six founder females paired and bred with first-cohort males during the second breeding season.

Stewart Island Robins came from the Freshwater Flats population on the mainland of Stewart Island (Fig. 1). Individuals were translocated on three separate occasions to Ulva Island. All released birds were color banded and closely monitored. Sixteen adult birds were released in September 2000. Five returned to their territories at Freshwater Flats, and six others disappeared and presumably died before breeding. A further four juveniles were released in January 2001 and 5 more in November 2001, of which two disappeared before breeding.

Over the course of the study on Ulva (2000–2007), all but one robin offspring ($n = 461$) were color banded as fledglings, which provided me with essentially complete data regarding pedigree relationships (0.2% unknown parents). For saddlebacks, the origin of 17 juveniles that fledged and survived from the initial 2000–2001 cohort was unknown, but with the aid of 12 microsatellite markers developed for a paternity study (Taylor et al. 2008), the unknown offspring were assigned to six breeding pairs with >90% confidence through the use of an assignment program that incorporates information about known pairs of male and female breeders (Dodds et al. 2005). Similarly, 17 of 27 juvenile saddlebacks of unknown origin from the 2001 to 2002 cohort were assigned among 14 breeding pairs (S. Taylor, K. Dodds, and I.J., unpublished data). The remaining 10 juveniles were either assigned to parents with 30–70% confidence with the assignment program, or their parentage was left unassigned. Because neither approach substantially changed the overall level of inbreeding or genetic founders for saddlebacks, I present only results of the assigned parentage. Since the 2002 breeding season, virtually all saddleback offspring (97.5%, $n = 318$) have been banded in the nest or in their natal territory; thus, only eight offspring (2.0%, $n = 403$) in the pedigree had unassigned parents.

Reintroduction of Robins and Takahe to Tiritiri Island

Prior to the 1800s, Tiritiri's mature broadleaf forest was extensively cleared by Maori. Between 1855 and 1971,

the island was grazed by sheep and cattle. In 1983 an extensive forest restoration program began. At the time of the robin and Takahe reintroductions in the early 1990s, the island had several small patches (15 ha total) of forest in the early stage of regeneration that would support robins and a larger grassland area (105 ha total) that would support Takahe. Full descriptions of the vegetation type and forest patches are in Ryan and Jamieson (1998) and Armstrong and Ewen (2002).

Forty-four banded North Island Robins were translocated from the central North Island forests near the city of Rotorua (Fig. 1) to Tiritiri in April 1992, and 14 more were translocated in June 1993 (Armstrong 1995). Of the 33 birds that survived to the start of the first breeding season (1992–1993), 7 were female. (It was unknown at the time of the first translocation that first-year male robins on North Island have delayed plumage maturation and therefore look like females [Armstrong 2001].) Another translocation in 1993 brought the number of released, living adults at the beginning of the second breeding season (1993–1994) to 12 females and 21 males (Armstrong & Ewen 2002). The robin population was monitored by D. Armstrong (Massey University) and students, and I derived the pedigree data (1992–2003) from a published analysis of inbreeding depression in this population (Jamieson et al. 2007). Fifty-one (7.9%) of 461 offspring had unknown parents in the pedigree.

In contrast to robins (average 35 g) and saddlebacks (average 75 g), which are relatively small forest passerines, Takahe are a large (average 3000 g) flightless rail that feeds mostly on grasses. Between 1984 and 1989, 25 Takahe were translocated from the alpine grasslands in the Murchison Mountains to three protected, offshore, lowland islands (Maud, Mana, and Kapiti) between the South and North islands (Fig. 1), where introduced pests and predators had been eradicated. The details of the island translocations and the extent of inbreeding across all four sites are documented elsewhere (Jamieson et al. 2003; Grueber & Jamieson 2008). Here, I compared inbreeding of the Tiritiri Island population of Takahe with inbreeding of robins and saddlebacks on Tiritiri and Ulva islands.

Two male and one female juvenile Takahe raised on Maud Island were translocated to Tiritiri in 1992. One of the males and the female were related, and they paired and bred. Two more unrelated pairs were introduced and bred in 1994, and three additional unrelated males were introduced between 1995 and 1997 (Department of Conservation, unpublished data).

Estimating Inbreeding with Pedigrees

Assuming that the adults attending a nest were the parents, I constructed pedigrees of the robin and saddleback populations. Molecular studies of saddlebacks and robins on Ulva Island, Tiritiri Island, and elsewhere in-

dicate that extrapair fertilizations either do not occur or are extremely rare in both species (Ardern et al. 1997; Taylor et al. 2008). Extrapair fertilizations also are rare or do not occur among territorial Takahe, so resident birds are almost certainly the parents of any offspring (Lettink et al. 2002; Grueber 2005). Takahe occasionally breed in groups of two (unrelated) adult males or two adult females. In one such two-male group on Tiritiri, paternity of two offspring could not be determined by molecular means. Thus, I assigned paternity randomly between the two males, which is biologically justified on the basis of parentage analysis of other breeding groups of Takahe (Grueber 2005).

I used the genetic-management software package Population Management 2000 (Pollak et al. 2002) to calculate inbreeding coefficients (f) for individuals of all four species. The program also calculates kinship coefficients (k) for breeding pairs, which are equal to the f of their (hypothetical) offspring. I constructed pedigrees that either excluded or included individuals with unknown parents and present kinship coefficients derived from both, as recommended by Ewing et al. (2008). I evaluated the following interrelated founder population statistics: number of genetic founders (individuals at the top of the pedigree that bred on the resident islands and produced at least one living descendent); retained gene diversity (proportion of heterozygosity in the source population retained in the descendent population); founder representation (proportion of genes in the living descendants that are derived from each founder); and founder genome equivalents (the number of genetic founders that would give rise to the gene diversity in the current population, assuming each founder contributed equally and there was no random loss of alleles across generations). The latter quantifies the cumulative loss of genetic diversity since the founder generation (Lacy 1995). Finally, although generation time in robins is half the generation time (4 years) in saddlebacks and island Takahe (8 years), all species showed extensive overlap in generations during the early growth stages of the population. For example, a founding male robin on Ulva paired with his great-great granddaughter.

Projected Rates of Inbreeding

To project future rates of inbreeding, I required estimates of the effective population size at carrying capacities for the study populations on both islands. Population models that include density dependence (I.J. & D. Armstrong, unpublished data) predict that robins and saddlebacks on Ulva will reach carrying capacities of 100 and 50 breeding pairs, respectively. Assuming Tiritiri robins are restricted to the current area of forest, the growth of that population should stabilize at about 40 breeding pairs (Dimond & Armstrong 2007). The Takahe population on Tiritiri is likely to stabilize at about five breeding pairs (I.J.,

unpublished data). I doubled the number of breeding pairs at carrying capacity to provide an estimate of effective population size (N_e). I then calculated the subsequent increase in F per generation with the following equation (Frankham et al. 2002):

$$F_t = 1/(2N_e) + [1 - 1/(2N_e)]F_{t-1},$$

where F_t is the level of inbreeding in the next generation. Starting with the current level of inbreeding and assuming that each population remained at its specified carrying capacity, I projected the number of years it would take for the four populations to become highly inbred—defined here as a mean $F = 0.1875$, which is equivalent to the population being more inbred, on average, than the matings of half-sibs ($F = 0.125$).

Results

Individuals Released and Pattern of Inbreeding

Of the 58 North Island Robins released on Tiritiri Island, 25 survived and successfully bred. Because the area of regenerating forest was initially small (15 ha), the breeding population stabilized at about 65 robins (~32 pairs) by 1997. After 1997, vegetation regeneration allowed the population to expand again (Fig. 2a). The frequency of close inbreeding ($k = 0.25$) on Tiritiri was initially high (3 of 13 new pairs in 1995), but the mean level of inbreeding

declined after one member of each of the three closely related pairs died in successive years (1997, 1998, and 2002) (Fig. 2a). Excluding individuals of unknown parentage from the pedigree changed the level of inbreeding only marginally (Fig. 2a).

For Stewart Island Robins, 12 of the 20 released birds (excluding the five that returned to their original breeding territories on Stewart Island) survived and attempted to breed on Ulva Island. Once first-generation birds started breeding and the population grew, the mean level of inbreeding for breeding pairs increased gradually (Fig. 2b), even though the number of closely related pairs ($k = 0.25$) was relatively small (one pair in 2004 and two pairs in 2005 and 2006). The level of inbreeding among robin pairs on Ulva eventually reached three times the level among robin pairs on Tiritiri in half the time (Figs. 2a-b).

Of the 30 South Island saddlebacks released on Ulva Island, 18 subsequently bred and produced offspring. As the population grew, the mean level of inbreeding remained low (Fig. 2c); only two breeding pairs were closely related ($k = 0.25$). Again, excluding the small number of individuals for which I did not know their parentage changed the level of inbreeding only marginally (Fig. 2c).

The Tiritiri Takahe population was initially founded by two related Takahe ($k = 0.125$). This pair bred the following year, and over the next 6 years produced four

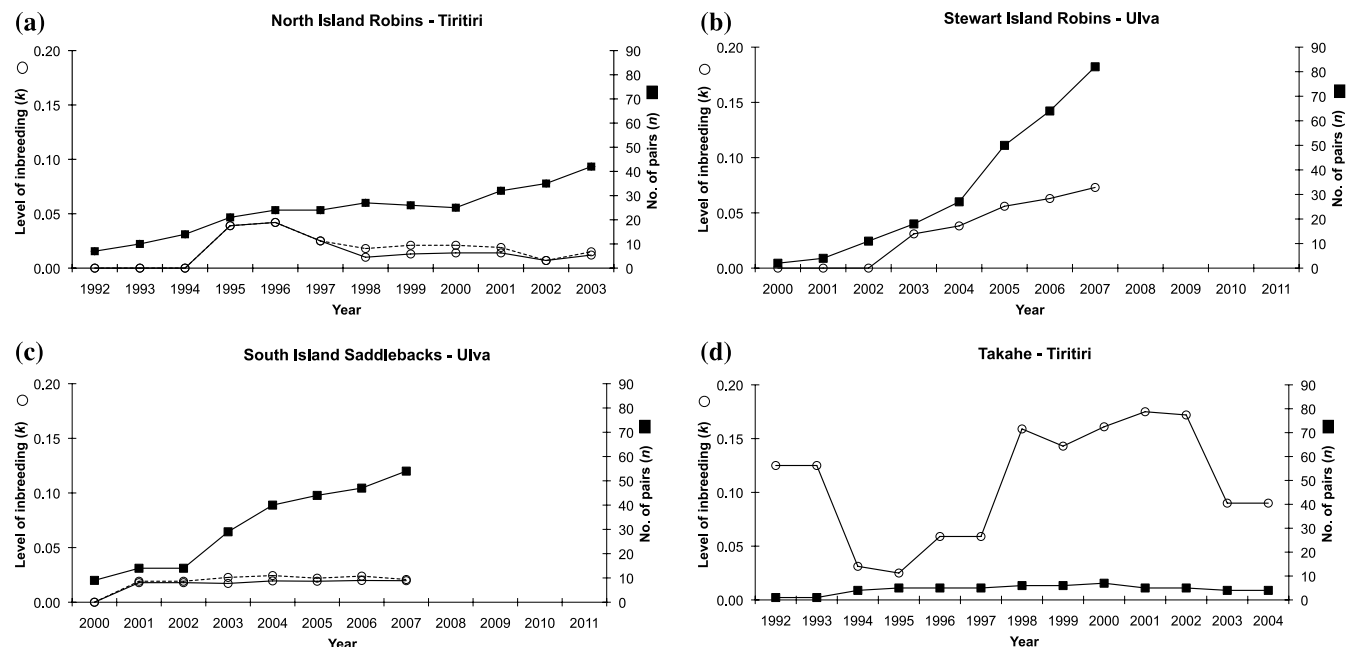


Figure 2. Changes in level of inbreeding and number of breeding pairs over time in four reintroduced island populations of (a) North Island Robins on Tiritiri, (b) Stewart Island Robins on Ulva, (c) South Island Saddlebacks on Ulva, and (d) Takahe on Tiritiri (unshaded circle, k of breeding pairs; shaded square, n of breeding pairs; dashed line, estimated levels of inbreeding when individuals with unknown parents are excluded from the pedigree). The initial breeding pair of Takahe released on Tiritiri were related.

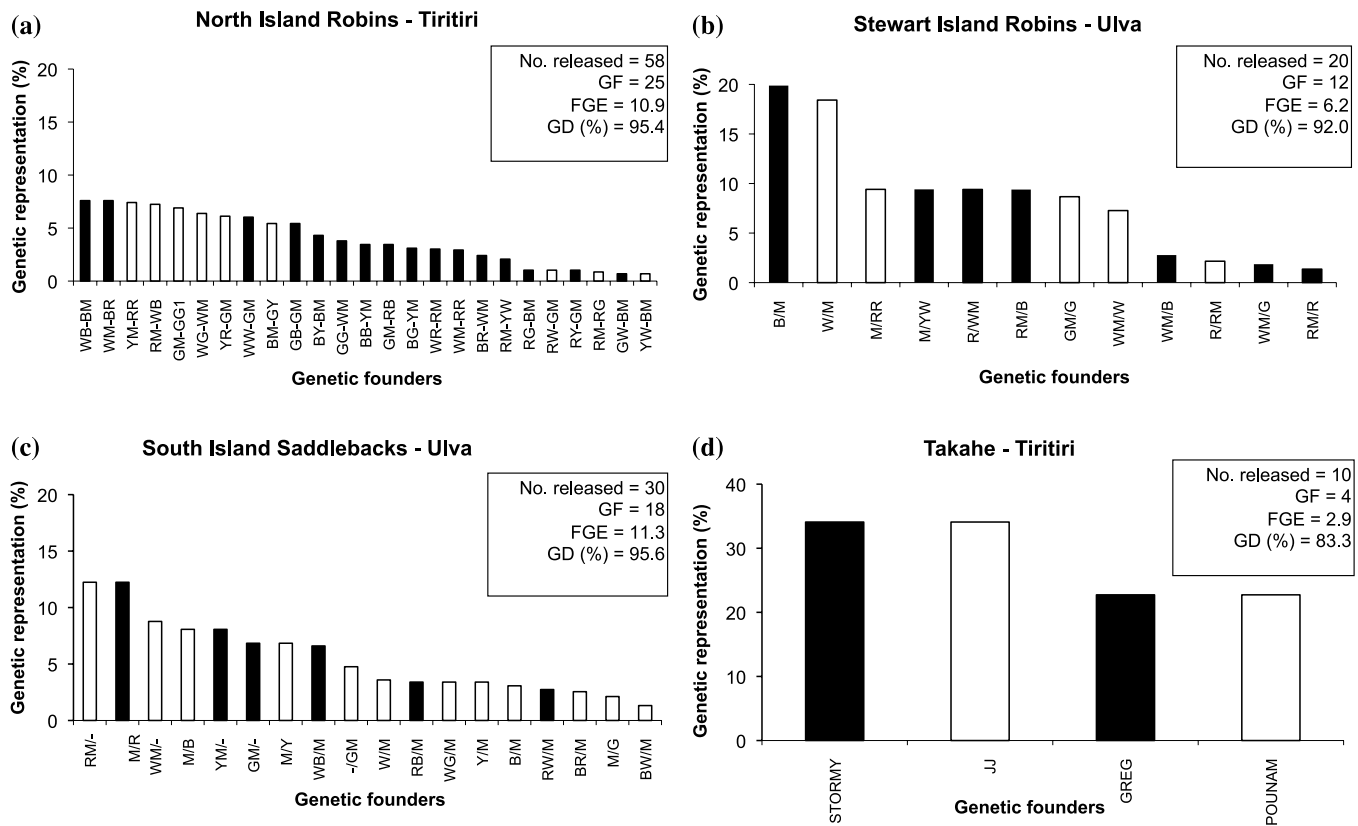


Figure 3. Percent genetic representation of each genetic founder in the descendants after seven breeding seasons for four reintroduced island populations of (a) North Island Robins on Tiritiri, (b) Stewart Island Robins on Ulva, (c) South Island Saddlebacks on Ulva, and (d) Takahē on Tiritiri (shaded bar, male; unshaded bar, female; GF, genetic founder; FGE, founder genetic equivalents; GD, retained genetic diversity; see text for definitions of terms).

offspring that eventually became breeders (in some cases breeding with each other), which may explain a relatively rapid increase in the mean level of inbreeding (Fig. 2d). The decline in the mean level of inbreeding in 1994 and 1995 was associated with the transfer of six unrelated breeders to the island. Subsequent large increases (e.g., 1998) and decreases (2003) in the mean annual rate of inbreeding were associated with the formation or breakup of closely related pairs ($k = 0.25$). The high rate of close inbreeding was partly a consequence of the relatively small population size, which averaged only five breeding pairs over a 13-year period (Fig. 2d).

Genetic Founders and Founder Genome Equivalents

The lower overall rate of inbreeding of the robin population on Tiritiri compared with Ulva (Fig. 2) was likely due in part to the larger number of birds released on Tiritiri (58) versus Ulva (20), which resulted in twice the number of genetic founders on Tiritiri (24) than on Ulva (12) when both populations are compared over a similar number of breeding seasons (Figs. 3a-b). The sex ratio of the genetic founders on Tiritiri was highly biased (16 males to 9 females) (Fig. 3a), which would have contributed to the

reduction in founder genome equivalents and gene diversity (Fig. 3a), whereas the sex ratio of genetic founders on Ulva was less biased (seven males to five females). Nevertheless, founder representation in the living descendants on Ulva was more skewed than on Tiritiri. One founding pair (Fig. 3b) contributed twice the proportion of genes of any other founding male or female on Ulva. This uneven genetic founder representation corresponded with the rise in inbreeding in Ulva robins (Fig. 2b) and the relatively low number of founder genome equivalents (6.2) and low retention of founder gene diversity (92.0%) (Fig. 3b). Tiritiri's robins had a relatively high loss of potential gene diversity given that of the 58 robins released on Tiritiri only 25 (43%) were genetic founders. From the 25, 10.9 founder genome equivalents contributed to the genetic diversity after seven breeding seasons, which suggested a relatively high loss of potential gene diversity. That is, the amount of genetic diversity in the Tiritiri robin population 7 years after the translocation was theoretically equivalent to only about 11 equally contributing founders. By contrast, the number of founder genome equivalents (11.3) and retained gene diversity (95.6%) for saddlebacks on Ulva was nearly equal to that of robins on Tiritiri, even though only 30 saddlebacks were released

(Fig. 3c). With only four genetic founders, Takahe on Tiritiri had the lowest number of founder genome equivalents (2.9) and the lowest retained gene diversity (83.3%) (Fig. 3d). Only a minority of the Takahe that were originally released produced any living descendents (40%, $n = 10$) over seven breeding seasons.

Projected Rates of Inbreeding

I estimated that the North Island Robin population on Tiritiri will become highly inbred (mean $F = 0.1875$) 100 years before the Stewart Island Robin population on Ulva, despite the lower initial inbreeding in the Tiritiri population (Fig. 4). The rate of increase in mean inbreeding was similar for saddleback and robin populations on Ulva (Fig. 4) because the lower abundance of saddlebacks (half that of robins) was offset by the robin's shorter generation time (half that of saddlebacks). With a generation interval equivalent to that of saddlebacks, the relatively small population of Takahe on Tiritiri will reach a mean of $F = 0.1875$ in <8 years.

Discussion

The increase in inbreeding and the associated loss of gene diversity (i.e., expected heterozygosity) over the initial phase of the reintroduction varied substantially among the four species, primarily because numbers of founders differed, sex ratio were biased, and breeding success was skewed. If the study populations reach their carrying capacity, differences in rates of inbreeding will primarily be a function of differences in abundance (compare the two robin species in Fig. 4).

The loss of genetic diversity associated with inbreeding and drift has two important consequences: it reduces the ability of populations to adapt to environmental change and it can result in a direct and immediate loss in fitness through inbreeding depression (Keller & Waller 2002).

Here, I discuss the effects of inbreeding and loss of genetic variation in terms of loss of adaptive potential.

The potential for loss of genetic variation in captive-breeding programs of vertebrates (such as those in association with zoos) is apparent because founder, and especially descendent, population sizes are typically small. The potential for loss of genetic variation in island reintroduction programs is not as apparent because descendent populations can be larger than those normally associated with captive breeding facilities. Furthermore, it could be perceived that reintroduced populations are unlikely to lose considerable genetic diversity because the species would have existed naturally on islands before it was extirpated. Nevertheless, most populations that occurred naturally on islands in the past would not have been closed because much larger populations on the adjacent mainland would have functioned as a source of intermittent gene flow from dispersing individuals. This is no longer the case in New Zealand because most mainland populations have been either extirpated (e.g., saddlebacks and Takahe) or occupy only a fraction of their former range (e.g., robins) (Innes et al. 2010). The fact that species must be reintroduced to these islands suggests their populations are likely to be closed and therefore that rates of inbreeding will increase (Frankham et al. 2002). Long-term monitoring of a population of Mauritius Kestrel (*Falco punctatus*), the only other detailed pedigree study of a threatened species reintroduced to an island, also showed increased inbreeding and loss of genetic diversity over time (Ewing et al. 2008).

Traditional captive breeding programs strive to maintain genetic diversity relative to the wild population by capturing a sufficient number of founders and subsequently selectively breeding individuals that are genetically underrepresented (see Haig et al. 1990). The goal of most reintroduction programs is to provide sufficient genetic diversity to allow the population to experience natural selection, assuming the founding

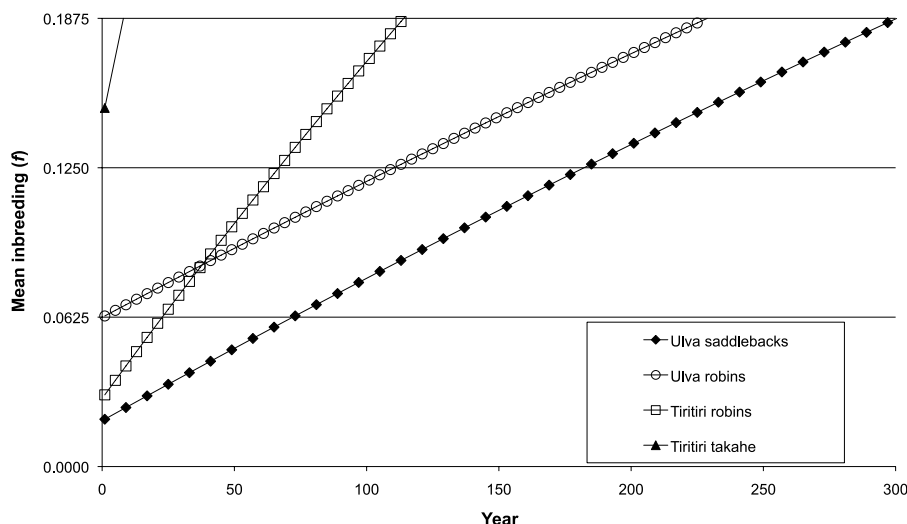


Figure 4. Mean inbreeding over time once carrying capacity is reached in four reintroduced island populations: South Island Saddlebacks on Ulva ($N_e = 100$), Stewart Island Robins on Ulva ($N_e = 200$), North Island Robins on Tiritiri ($N_e = 80$), and Takahe on Tiritiri ($N_e = 10$). Generation intervals are 4 years for robins and 8 years for saddlebacks and Takahe.

population can grow quickly. Therefore, adequate abundance of founders is needed at the initiation of reintroduction to minimize loss of genetic diversity, although the source population itself may have already lost considerable genetic diversity (e.g., saddlebacks; Taylor et al. 2007). For example, 20 founder genome equivalents would contain 97.5% of the genetic variation of the wild population from which the founders were drawn, which would assure sufficient founder variability was present at the outset of a recovery program to allow long-term (100–200 years) retention of 90% of genetic variation (Soulé et al. 1986; Lacy 1994, 1995). Determining the minimum number of individuals needed for release (assuming there are constraints on time, resources, and costs) to ensure 20 genetic founder equivalents depends on the life-history traits and likely postrelease survival rate of the species in question. Programs in New Zealand have tended to target 20–40 birds for reintroductions to offshore islands to ensure there are sufficient numbers of survivors to establish a population, but not necessarily to ensure maintenance of genetic diversity (Taylor et al. 2005). My results indicate that only 40–60% of the released birds ($n = 10$ –58) had at least one living descendent after seven breeding seasons. Given that some individuals are certain to die after release, an uneven sex ratio, and skewed breeding success (i.e., unequal founder representation), my results showed that releasing 20–60 robins or saddlebacks yielded only about 6–11 founder genome equivalents or 92–96% retention of the founder gene diversity after seven breeding seasons. Current reintroductions in New Zealand and elsewhere are likely to be limited in their capacity to manage close inbreeding and equalize founder representation over the short term in unmanaged populations. Although it is possible to minimize the opportunity for close inbreeding and genetic drift by releasing larger numbers of individuals, the inevitable long-term accumulation of inbreeding in closed populations, as I found here, can be addressed effectively only by avoiding reintroductions to islands of a small size or by periodically introducing new genetic stock to the island.

The latter strategy has been recommended for managing Takahe on offshore islands, including on Tiritiri (Grueber & Jamieson, 2008). Nevertheless, because the island populations of Takahe are close to their carrying capacity, there is an increased probability that newly introduced individuals will not recruit into the breeding population. Therefore an initial action of translocating surplus and genetically overrepresented Takahe back to Fiordland (where the population is below carrying capacity) has been adopted recently (Wickes et al. 2009).

With an increasing number of reintroductions being conducted on much smaller scales than those I describe here, many of them are unlikely to have the resources for genetic restocking from source populations and frequent transfers between protected areas to minimize the

loss of genetic variation over the long term. My results suggest the need for better integration of reintroductions into long-term management programs of highly threatened species to be consistent with a goal of minimizing inbreeding and maintaining genetic diversity in reintroduced populations.

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