

Moderate inbreeding depression in a reintroduced population of North Island robins

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Abstract

Reintroductions of threatened species are increasingly common in conservation. The translocation of a small subset of individuals from a genetically diverse source population could potentially lead to substantial inbreeding depression due to the high genetic load of the parent population. We analysed 12 years of data from the reintroduced population of North Island robins *Petroica longipes* on Tiritiri Matangi Island, New Zealand, to determine the frequency of inbreeding and magnitude of inbreeding depression. The initial breeding population consisted of 12 females and 21 males, which came from a large mainland population of robins. The frequency of mating between relatives ($f > 0$; 39%, $n = 82$ pairs) and close relatives ($f = 0.25$; 6.1%) and the average level of inbreeding ($f = 0.027$) were within the range reported for other small island populations of birds. The average level of inbreeding fluctuated from year to year depending on the frequency of close inbreeding (e.g. sib-sib pairs). We found evidence for inbreeding depression in juvenile survival, with survival probability estimated to decline from 31% among non-inbred birds ($f = 0$) to 11% in highly inbred juveniles ($f = 0.25$). The estimated number of lethal equivalents based on this relationship (4.14) was moderate compared with values reported for other island populations of passerines. Given that significant loss of fitness was only evident in highly inbred individuals, and such individuals were relatively rare once the population expanded above 30 pairs, we conclude that inbreeding depression should have little influence on this robin population. Although the future fitness consequences of any loss of genetic variation due to inbreeding are uncertain, the immediate impact of inbreeding depression is likely to be low in any reintroduced population that expands relatively quickly after establishment.

Introduction

Inbreeding depression, defined as the loss of fitness due to mating between close relatives, is well documented in laboratory, agricultural and zoo populations, but until recently was thought to be rare in wild populations (Crnokrak & Roff, 1999). Studies reporting extensive inbreeding depression in natural populations are on the increase, suggesting that inbreeding depression may be more common than previously thought (see reviews in Crnokrak & Roff, 1999; Keller & Waller, 2002), but the overall number of well-documented cases is still small. The best evidence of inbreeding depression has come from studies of birds, especially monogamous species living on islands, but there have only been 14 published studies over the last 30 years (see table 2 in Kruuk, Sheldon & Merilä, 2002).

Part of the difficulty of detecting inbreeding depression in wild populations is that it is difficult to obtain reliable long-

term pedigree data, and inferences from genetic data such as observed heterozygosity may be unreliable (Balloux, Amos & Coulson, 2004; Pemberton, 2004; Slate *et al.*, 2004). Even when reliable pedigrees are available, the frequency of inbreeding might be low, possibly due to the evolution of inbreeding avoidance mechanisms in many organisms (Pusey & Wolf, 1996), leading to low statistical power. Despite these limitations, the picture that is emerging is that inbreeding depression can be substantial in wild populations of plants and animals and can be severe enough to affect the viability of small populations (Crnokrak & Roff, 1999; Keller & Waller, 2002).

A pedigree study of a large island population of collared flycatchers *Ficedula albicollis* in Sweden reported a very low frequency of inbreeding, but when it did occur, the level of inbreeding depression was the highest ever recorded in a wild population of birds (Kruuk *et al.*, 2002). The significant inbreeding depression was presumably due to the island

population's substantial genetic load, that is, the high load of deleterious alleles normally associated with a population with high immigration rates and low frequency of inbreeding. Kruuk *et al.* (2002) argued that their results had important conservation implications, should such large populations crash in the future and thus be exposed to inbreeding depression.

The reintroduction of threatened species from a relatively genetically diverse source population to a small island refuge simulates a population going through a sudden crash or bottleneck, particularly when only a small subset of individuals from the source population are translocated and released. Such populations could potentially undergo substantial inbreeding depression while the initial population size is small, lowering the chances of successful population establishment. Translocations are a commonly used tool in conservation management of threatened species (Griffith *et al.*, 1989; Armstrong & McLean, 1995; IUCN, 1998); yet, only two studies that we are aware of have measured the extent of inbreeding depression in newly reintroduced populations (Jamieson, Roy & Lettink, 2003; Swinnerton *et al.*, 2004). In both these cases, high levels of background inbreeding in the source populations might have made the detection of inbreeding depression difficult because the relatedness of the founders would be underestimated and possibly because the source population may have had reduced genetic load.

Translocations from larger, more genetically diverse source populations to small island refuges are expected to show greater evidence of inbreeding depression, a prediction we examine in a reintroduced island population of North Island robins *Petroica longipes*, a small New Zealand forest passerine. We determine the frequency of inbreeding and its effects on fitness parameters and estimate the genetic load in a relatively small population of robins reintroduced to Tiritiri Matangi Island (220 ha) in 1992. This particular population is well suited for pedigree analysis not only because of the reliability and depth of the pedigree (see below), but because the pedigree begins when the island population was first established. We structured our analysis after that of Kruuk *et al.* (2002) and Keller *et al.* (2002) to estimate the number of lethal equivalents (Morton, Crow & Muller, 1956), so that we could compare our estimate of genetic load with those of other island populations of birds.

Study area and methods

Breeding biology and conservation status

The North Island robin is a small (~30 g) ground-feeding insectivore that is highly sedentary, remains on its territory year-round and rarely changes mates. They settle on territories within a few months of fledging and breed in their first year if they can attract a mate (Armstrong *et al.*, 2000). They breed as pairs and are sexually monogamous. A molecular study of robins on Tiritiri Matangi found no evidence of extra-pair fertilizations in 29 offspring across 16 families (Ardern *et al.*, 1997b). Similar findings have been found for

74 families sampled across five populations of the South Island robin *Petroica australis* (Ardern *et al.* 1997b; S. Taylor, S. Bossenkool, & I. Jamieson, unpubl. data). North Island robins have a modal clutch size of two (range 1–3) and most females attempt to breed at least twice a year (Armstrong *et al.*, 2000). Male North Island robins have delayed plumage maturation, and unless they are paired and their behaviour is observed, individuals cannot be reliably sexed until after their first breeding season (Armstrong *et al.*, 2000; Powlesland, 2002). North Island robins are rare and are generally in decline on the mainland as a consequence of habitat loss and predation by exotic mammals (Heather & Robertson, 1996). They have now been reintroduced to six islands following predator eradication or habitat regeneration, and have also been reintroduced to 11 mainland 'island' areas with ongoing predator control (Armstrong, 1999–2006; Armstrong, 2000).

Study population

Tiritiri Matangi (36°36'S, 174°53'E) is a 220 ha island in the Hauraki Gulf, 3.5 km east of Whangaparoa Peninsula and 28 km north of Auckland. The island was originally covered by broadleaf forest and would have been occupied by robins (Drey *et al.*, 1982). Before the 1800s, the forest was extensively cleared by Maori, who also introduced Pacific rats or kiore *Rattus exulans*. The island was then used for grazing sheep and cattle by European farmers between 1855 and 1971, but has now undergone an extensive regeneration programme, eradication of rats and reintroduction of several native birds (Armstrong, 1999–2006). At the time of the reintroduction, the island was at the early stages of regeneration, and consisted of several small patches of forest totalling about 15 ha that would support robins. Full descriptions of the vegetation type and forest patches can be found in Armstrong *et al.* (2000) and Armstrong & Ewen (2002).

The source birds were taken from Mamaku Plateau (38°4'S, 175°80'E) near the city of Rotorua. The robins were caught over an area of about 10 000 ha of pine plantation and native forest, with good connection to additional forest covering about 100 000 ha. Based on the densities found during capture, it is likely that the population over this large forest area is over 10 000 birds. The estimated band-sharing coefficient of translocated birds was 0.20 (Ardern *et al.*, 1997b), which was substantially lower than the coefficients found in bottlenecked populations of South Island robins (Ardern *et al.*, 1997a,b). Forty-four robins were translocated from Mamaku to Tiritiri Matangi in April 1992, and a further 14 robins were translocated in June 1993 (Armstrong, 1995). It was subsequently learned that males have delayed plumage maturation and that the sex ratio was biased against females at the time of release (Armstrong, 2001). Of the 33 birds that survived to the start of the first breeding season (1992–1993), only seven were females. All seven females acquired mates but only two successfully fledged young (two each) in the first breeding season. The follow-up translocation in 1993 increased the number of released adults alive at the beginning of the second breeding

season (1993–1994) to 12 females and 21 males (Armstrong & Ewen, 2001). The breeding population reached a carrying capacity of about 65 birds by 1996/1997 (Armstrong & Ewen, 2002), but subsequent habitat regeneration allowed the breeding population to increase to about 90 birds by 2003 (Dimond & Armstrong, 2006).

Monitoring

All forest patches were surveyed at the beginning (September) and near the end (January) of each breeding season to obtain resighting data for modelling survival. Most offspring were banded in the nest, and birds that were not banded in the nest were excluded from survival analysis. Breeding monitoring consisted of visiting pairs to determine whether they were nesting, and then to band young and to count fledglings. Hatching success was not always recorded, but the number of fledglings was accurately recorded for each monitored pair. Robins appear reluctant to fly across open water and there have been no known cases of banded birds from the island being sighted on the nearest point on the mainland, *c.* 3.5 km away. Thus our data on survival were unlikely to be biased by undetected dispersal events. Further details of how nests were found and monitored are described elsewhere (Armstrong & Ewen, 2002; Dimond & Armstrong, 2006).

Pedigree construction and inbreeding/fitness analysis

We constructed pedigrees of the robin population assuming that the adults attending a nest were the genetic parents (see above). Inbreeding coefficients (f) for individual birds and kinship coefficients for breeding pairs ($= f$ of their offspring) were calculated using PEDSYS (South-west Foundation for Biomedical Research, San Antonio, TX, www.sfbr.org) with the Stevens–Boyce algorithm option (Boyce, 1983). All inbreeding and kinship coefficients are relative to the founding birds introduced in 1992 and 1993. As is now standard practice (e.g. Keller *et al.*, 2002; Kruuk *et al.*, 2002; Marshall *et al.*, 2002), we allowed for the effects of varying pedigree depth as the study progressed by including only offspring for which all four grandparents were known. Restricting the analysis to offspring for which all eight great-grandparents were known resulted in too small a sample size and would have omitted most known cases of close inbreeding. The inbreeding analysis covered the years from 1994 to 2003, excluding 1997, when no nestlings were banded.

We used generalized linear models fitted with an appropriate error structure to account for the effect of inbreeding coefficients (f) on various fitness parameters. More specifically, we examined:

(i) *Juvenile survival*: The probability of juveniles surviving from fledging until the following breeding season (September) was modelled using Program MARK (White & Burnham, 1999). Individual inbreeding coefficients were included using an individual covariate, and the log link used to fit the model $\ln(S_i) = \ln(S_0) + Bf$. The parameter B provides an

estimate of the number of lethal equivalents in a haploid genome (Morton *et al.*, 1956). MARK provides maximum likelihood estimates of S_0 and B that are identical to those obtained with Kalinowski & Hedrick's (1998) method. However, MARK allows a much wider range of models to be fitted, including those where resighting probability is accounted for. We used the live recaptures option in MARK to obtain separate estimates of survival and resighting probability for juveniles and adults (birds were considered to become adults at the start of the next breeding season). Following Dimond & Armstrong's (2006) results for juvenile survival in this population, we initially allowed resighting probability to be fully time dependent, and modelled temporal variation in juvenile survival as a function of the number of pairs at the start of the breeding season. We then considered simpler models where these factors were removed. We also fitted a model where individuals were divided into six groups based on inbreeding coefficients, and use this to assess the form of the relationship between juvenile survival and inbreeding.

(ii) *Individual reproductive success*: For the individuals that survived their first season, the numbers of fledged offspring they produced over the years of the study was analysed as a Poisson errors model with a log-link function, and included cohort as a categorical variable and age as a covariate to correct for differences in longevity. We also looked for an effect of inbreeding on the proportion of fledged offspring that became breeders (i.e. recruited into the breeding population) treating the proportion as a binomial errors model, with the number of fledglings as the binomial denominator and a logit link function. The sex of these birds was known and was included as a categorical variable, but did not improve the overall model and therefore was omitted from the final analysis.

(iii) *Pair reproductive success*: The annual number of fledglings produced by a pair was analysed as a least squares linear regression, with pair ID entered as a random effect variable, year as a categorical variable and maternal and paternal inbreeding coefficients and the pair's kinship coefficients as covariates. The proportion of fledged offspring that became breeders was also analysed as a binomial errors model, with the number of fledglings as the binomial denominator and a logit link function, and included the total number of years the pair bred together as a covariate to control for variation in breeding experience.

Except for the analysis of juvenile survival, all statistical analyses, including calculating odds ratios and confidence intervals (CI), were performed with JMP (version 6.0).

Results

Frequency and pattern of inbreeding

The total number of unique breeding pairs in the study was 160, of which 20.6% were pairings between relatives ($f \geq 0$) and 3.1% were between close relatives ($f = 0.25$), yielding an average level of inbreeding of 0.014. Including only those individuals with four known grandparents, the number of

pairs declines to 82, of which 39.0% involved relatives and 6.1% involved close relatives, giving an average level of inbreeding of 0.027. As shown in other studies (e.g. Keller, 1998), deriving mean inbreeding values from all pairs underestimates the true level of inbreeding (see Fig. 1) because the ancestry of the founding birds is unknown but assigned $f=0$. Because of this bias, we included only those individuals for which all four grandparents were known in the analyses below.

Annual fluctuations in the level of inbreeding (Fig. 1) were primarily due to variation in the incidents of close inbreeding (i.e. high kinship coefficients = 0.25). For example, the average level of inbreeding was the highest in 1995 when three of nine pairs (with known grandparents) were brother–sister pairings. Thereafter, the number of closely related pairs declined to two in 1996 and one in 1997–2001. There were no closely related pairings in 2002–2003 and hence average inbreeding declined again despite the overall frequency of related pairs increasing from 18% in 2000 to 59% in 2003.

Effects on fitness

Juvenile survival

We monitored 238 juveniles where all four grandparents were known, and 100 of these were inbred to some extent ($f>0$). Comparison of juvenile survival models gave clear evidence of inbreeding depression, as models with an inbreeding covariate had three to four times the support of similar models that excluded this covariate (Table 1). Population density was not a useful predictor of juvenile survival with this dataset; hence, the best model for juvenile survival

was a simple log-linear function of the inbreeding coefficient. Under this model, the parameter B (number of lethal equivalents) was estimated to be 4.14 (95% CI ranging from -0.36 to 8.65), and survival probability was estimated to decline from 31% for non-inbred ($f=0$) juveniles to 11% for highly inbred ($f=0.25$) juveniles (Fig. 2). There were insufficient data for different levels of inbreeding to assess the form of the relationship (Fig. 2). However, the data suggest little effect of inbreeding in moderately inbred birds ($f=0.002$ – 0.125), and these made up the majority (77%) of the 100 inbred birds.

The models used in the above analysis assumed constant re-sighting probability for both juveniles (estimated to be 0.77) and adults (estimated to be 0.91), as preliminary analysis indicated that this was more parsimonious than retaining time dependence in re-sighting probability. However, models with time-dependent resighting probability also indicate a clear effect of inbreeding.

Individual reproductive success

For those robins that survived their first season ($n=61$), there was no evidence that inbreeding coefficient had an effect on their reproductive success in terms of either the number of offspring they fledged or the proportion of fledglings that were recruited into the breeding population, after correcting for age and cohort (Table 2a). However, there were only two individuals of $f=0.25$ that survived their first year and subsequently bred; hence, the power to detect differences was low. Of these two birds, one fledged no offspring and the other fledged 10, of which three were recruited into the breeding population.

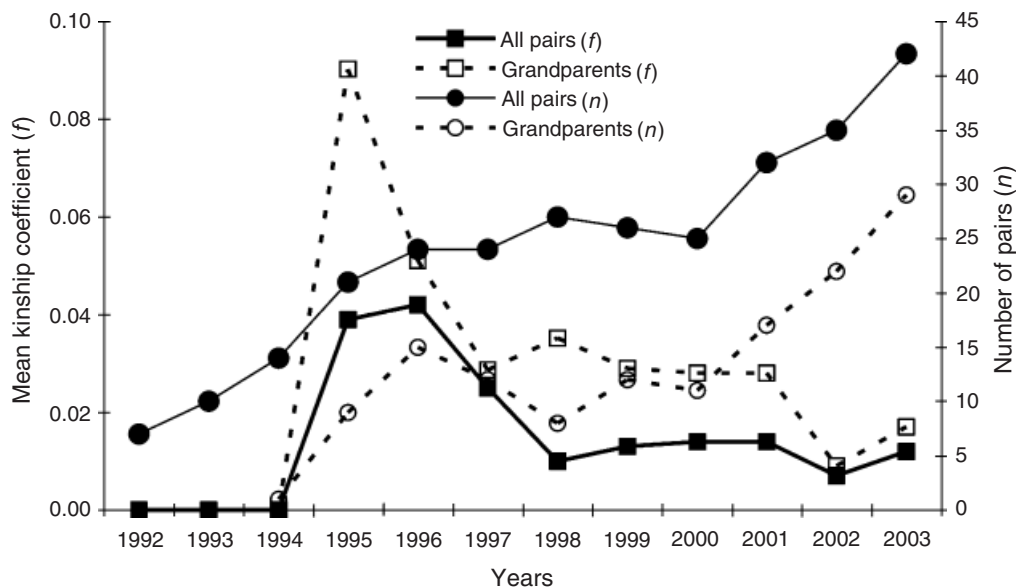


Figure 1 Annual changes in mean kinship coefficients of breeding pairs (f) corresponding to changes in the total number of pairs (n) for North Island robins *Petroica longipes* on Tiritiri Matangi Island. The solid lines show values based on all pairs, while the dashed line shows values for a subset of pairs with known grandparents only.

Table 1 Comparison of models to assess the effects of inbreeding (f) and population density (d) on juvenile survival (S)

Model ^a	K^b	AICc ^c	Δ_i^d	w_i^e
$\ln(S) = \ln(S_0) + Bf$	5	654.938	0.00	0.56
$\ln(S) = \ln(S_0) + Bf + Cd$	6	656.766	1.83	0.22
$\ln(S) = \ln(S_0)$	4	657.650	2.71	0.14
$\ln(S) = \ln(S_0) + Cd$	5	659.074	4.14	0.07

^aModels fitted to re-sighting data using live recaptures option in Program MARK.

^bNumber of parameters in the model, including one parameter for adult survival and two re-sighting parameters (for adults and juveniles).

^cCorrected Akaike' information criterion.

^dDelta AICc indicating difference in AICc value from that of the best model.

^eAkaike weight indicating relative support for the model.

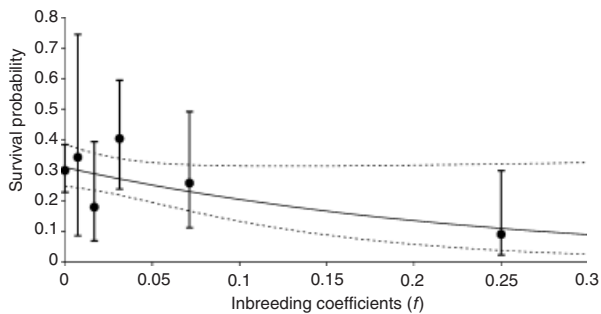


Figure 2 Probability of juvenile North Island robins *Petroica longipes* on Tiritiri Matangi Island surviving to adulthood in relation to their inbreeding coefficients. Points show estimated probabilities for different levels of inbreeding ($f=0$, $n=138$; $f=0.002-0.009$, $n=17$; $f=0.016-0.020$, $n=12$; $f=0.031$, $n=28$; $f=0.063-0.125$, $n=20$; $f=0.25$, $n=23$), with vertical bars showing 95% confidence limits. The solid line shows the model $\ln(S) = -1.17 - 4.14f$, which was fitted to data using Program MARK, and the dotted lines show the 95% confidence limits around this relationship.

Pair reproductive success

We also examined the effects of inbreeding on a pair's reproductive success, after controlling for the number of years that the pair had bred together. There was no evidence that the inbreeding coefficient of the male or female, or the kinship coefficient of the pair had a significant effect on annual fledgling production, but there was evidence that the kinship coefficient affected the proportion of fledglings that were recruited into the breeding population (Table 2b). The model predicts that a kinship coefficient of 0.25 would result in an 80.8% (95% CI = 11.5–96.5%) reduction in probability of recruitment into the breeding population relative to pairs with kinship coefficient = 0. However, this effect is partly due to the low first-year survival rate of inbred juveniles (see above).

Discussion

The frequency of matings between relatives ($f > 0$; 39%) and close relatives ($f = 0.25$; 6.1%) and the resulting average level of inbreeding ($f = 0.027$) in this small island population was substantially higher than that reported for a large island

population of collard flycatcher, but was within the range of that reported for other small island populations of birds (Table 3). The number of birds released during the first 2 years of the reintroduction was high relative to other avian translocations in New Zealand (Taylor, Jamieson & Armstrong, 2005), and therefore the rate of inbreeding might be lower than that of other island reintroduction programmes. Nevertheless, the average level of inbreeding was still high initially ($f = 0.09$), corresponding to a high proportion of new pairings between close relatives (in this case siblings). Thereafter, the incidence of close inbreeding declined as the population showed limited expansion, even though the overall frequency of inbreeding increased as is expected in a small closed population. The annual and overall frequency of inbreeding and close inbreeding in this robin population is what would be expected from a random mating pattern; that is, there was no evidence birds were avoiding inbreeding (I. Jamieson, unpubl. data). Other pedigree studies of island birds have also found little evidence of inbreeding avoidance (Gibbs & Grant, 1989; Keller & Arcese, 1998), but this is somewhat surprising in the robins' case, given their sedentary nature (Armstrong *et al.*, 2000) and moderate levels of inbreeding depression (see below). Overall, although the frequency of inbreeding was high for a wild population, the initial translocation of a total of 19 females and 39 males, and the inevitable mortality that followed, did not result in exceptionally higher levels of inbreeding than what would be expected in a natural island population of monogamous birds (Table 3).

The translocation of a small subset of birds from a large and genetically diverse source population simulates a population going through a sudden crash or bottleneck. Indeed, the pattern in annual changes in mean inbreeding coefficients for the robins on Tiritiri Matangi is remarkably similar to that shown by song sparrows *Melospiza melodia* on Mandarte Island after they had gone through a similar-sized bottleneck event associated with a harsh winter (Keller, 1998; Fig. 1). After a sudden decline in a population, it is predicted that the fitness effects of inbreeding should be immediate and significant, assuming the large source population is carrying substantial genetic load (Keller & Waller, 2002; Kruuk *et al.*, 2002). Our data support this prediction as we were able to detect significant inbreeding depression in the form of a lower probability of survival at the juvenile stage and lower offspring recruitment into the breeding

Table 2 Effects of inbreeding on reproductive success of (a) individuals and (b) breeding pairs measured in terms of fledgling productivity and proportion of fledglings recruited into the breeding population

Fitness parameter	Term	d.f.	χ^2 (or <i>F</i> -ratio)	<i>P</i>
(a) Individual reproductive success				
No. of fledglings (<i>n</i> =61)	Cohort	8	51.71	<0.001
	Age	1	65.87	<0.001
	<i>f</i>	1	0.18	0.67
No. of recruited/no. of fledged ^a (<i>n</i> =28)	Cohort	6	9.38	0.15
	Age	1	0.115	0.73
	<i>f</i>	1	0.019	0.89
(b) Pair reproductive success				
Annual no. of fledglings (<i>n</i> =123)	Year	8	0.83	0.57 (<i>F</i> -ratio)
	Paternal <i>f</i>	1	0.84	0.36
	Maternal <i>f</i>	1	2.02	0.16
	Pair's <i>f</i> ^b	1	0.34	0.56
No. of recruited/no. of fledged ^a (<i>n</i> =44)	Years bred	1	0.014	0.91
	Paternal <i>f</i>	1	0.0035	0.95
	Maternal <i>f</i>	1	1.99	0.16
	Pair's <i>f</i> ^b	1	5.30	0.021

^aOnly included pairs that first bred in 2001 or earlier.

^bPair's *f* is the kinship coefficient between a male and female pair and is equal to *f* of offspring produced by that pairing.

Table 3 Level of inbreeding and inbreeding depression (estimated by *B*, the number of lethal equivalents) for several wild populations of passerine birds living on islands.

Species	Latin name	Annual population size (<i>n</i>)	No. of pairs ^a	% Pairs <i>f</i> >0	% Pairs <i>f</i> =0.25	Mean <i>f</i>	<i>B</i>	Trait on which <i>B</i> was based	Reference
Collard flycatcher	<i>Ficedula albicollis</i>	662	2107	1.04	0.8	0.002	7.47	Juvenile survival	Kruuk <i>et al.</i> (2002)
Large ground finch	<i>Geospiza magnirostris</i>	18	57 ^b	62.0	61.0	0.154	4.47	Juvenile survival	Grant <i>et al.</i> (2001), Keller <i>et al.</i> (2002)
Cactus finch	<i>Geospiza scandens</i>	80	120	16.7	3.3	0.016	4.27	Juvenile survival	Keller <i>et al.</i> (2002)
North Island robin	<i>Petroica longipes</i>	24	82	39.0	6.1	0.027	4.14	Juvenile survival	This study
Song sparrow	<i>Melospiza melodia</i>	64	285	72.0	<7.6 ^c	0.051	1.32	Fledgling to first breeding	Keller (1998)
Great tits	<i>Parus major</i>	100	280	47.0	8.7	0.036	0.58 ^d	Egg to fledgling	van Noordwijk & Scharloo (1981)
Medium ground finch	<i>Geospiza fortis</i>	198	364	19.8	0.8	0.011	0	Juvenile survival	Keller <i>et al.</i> , (2002)

^aIncludes only those with known grandparents or where *f*>0.125 could be detected.

^bBased on two cohorts.

^cIncludes pairs with *f*=0.125.

^dValue was considerably lower for juvenile survival because of high recruitment of inbred offspring onto breeding territories.

Species are ranked in descending order according to their estimate of *B*. All species showed significant levels of inbreeding depression for various traits, and when more than one estimate of *B* was available, juvenile survival was chosen for comparative purposes. Values for North Island robins *Petroica longipes* are indicated in bold.

population of inbred individuals. We did not detect significant inbreeding depression in a pair's annual production of fledglings or an inbred individual's proportion of recruited fledglings, but in the latter case, detecting a significant trend would have been difficult, given that only two closely inbred individuals survived to breeding age. Closely inbred offspring (*f*=0.25) were estimated to have a 65% lower probability of survival relative to non-inbred birds, but there was no evidence of significant effects at lower levels of inbreeding. Based on the estimated number of lethal equivalents reported for other island populations of passerines, we

conclude that inbreeding depression in the Tiritiri Matangi population of robins was moderate to high (Table 3). This study plus others (e.g. Briskie & Mackintosh, 2004) also indicate that inbreeding depression in native New Zealand birds is more common than previously appreciated, and at least in this case, there is little evidence of purging of genetic load (see Jamieson, Wallis & Briskie, 2006).

On the other hand, not only did closely inbred birds make up a small fraction of the total population, but 70% of non-inbred juveniles also failed to survive to the first breeding season. Therefore, inbreeding appears to explain a relatively

small proportion of the overall variation in juvenile survival. Analysis of a more extensive dataset (i.e. including birds lacking pedigree information) has shown that juvenile survival is density dependent, and tightly constrained by the available habitat (Dimond & Armstrong, 2006). The low survival, and lack of apparent density dependence, in the analysis reported here reflects the fact that most of the data were from years with a relatively high density. We had no estimate of the negative effects of inbreeding on egg hatchability, although modelling has shown that lowered hatching success is likely to have only a slight effect on population growth rates in reintroduced robin populations (Taylor *et al.*, 2005).

Continuing maturation of the replanted forest should allow the robin population on Tiritiri Matangi to expand to several hundred birds over the next few decades (Dimond & Armstrong, 2006). Simulations using VORTEX predicted that the population had negligible chances of extinction over the next 100 years under the current conditions (Armstrong & Ewen, 2002). These projections did not take inbreeding depression into account. With no further releases, the overall proportion of inbred individuals should increase by $1/2n$ per generation (Frankham, Ballou & Briscoe, 2002), although closely inbred individuals ($f \geq 0.25$) are expected to remain uncommon. However, the level of close inbreeding could increase dramatically if the population were to go through a sudden crash. Nevertheless, a single translocation of 10–20 birds would presumably result in enough gene flow and heterosis to reverse any potential population decline due solely to inbreeding depression (e.g. Grant, Grant & Petren, 2001; Marr, Keller & Arcese, 2002).

More generally, although the future fitness consequences of any loss of genetic variation due to inbreeding are uncertain, the immediate impact of inbreeding depression *per se* on either the probability of establishment or subsequent extinction risk of reintroduced populations is likely to be low, as long as the population expands relatively quickly at low densities (Taylor *et al.*, 2005). The impact of inbreeding depression on reintroduced populations with slower growth rates and longer generation times, or in more stressful environments, is likely to be greater (Frankham *et al.*, 2002). Further data are required from long-term studies of marked individuals with known pedigrees to determine whether the patterns of inbreeding and inbreeding depression reported here are indicative of other reintroduced populations.

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