Sex-Specific Consequences of Recent Inbreeding in an Ancestrally Inbred Population of New Zealand Takahe

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Abstract: *Although the negative effects of close inbreeding in captive populations are well known, inbreeding in small, free-ranging populations is less well understood. During the mid-1980s, small numbers of the flightless Takahe (*Porphyrio hochstetteri*) were successfully translocated from the last remaining population in mountainous Fiordland to four island refuges. Previous research has shown that introduced island Takahe and their descendents lay significantly more infertile eggs and raise fewer juveniles per egg than Takahe in their native habitat in Fiordland. Here we first show that the remnant population of Takahe in Fiordland was likely to have been severely inbred. From this we hypothesize that further, recent inbreeding (based on four generations of pedigree data) by Takahe on islands should have negligible fitness consequences. This hypothesis is only partially supported. Mean hatching and fledging success has remained consistently low (<40% and 77%, respectively) and was not correlated with the rapid increase in the average inbreeding coefficient of island Takahe since 1991. Neither the inbreeding coefficient of a pair's offspring nor the inbreeding status of the breeding male had a significant effect on hatching or fledging success. Similarly, the inbreeding status of the breeding female had no significant effect on hatching success. However, the inbreeding status of the female did negatively affect fledging success. Why poor reproductive success was further exacerbated by inbreeding in females but not in males or pairs is unknown, although a similar pattern has been reported in an island population of Song Sparrows (*Melospiza melodia*). We speculate that the generally lower reproductive success that most island Takahe exhibit is a result of environment-dependent inbreeding depression. We conclude from our pedigree analysis that island Takahe are undergoing further inbreeding depression, but the reduction in fitness appears to be expressed in inbred females only.*

Consecuencias Sexo-Específicas de Endogamia Reciente en una Población Ancestralmente Endogámica de Takahe de Nueva Zelanda

Resumen: *Aunque los efectos negativos de la endogamia en poblaciones cautivas son bien conocidos, la endogamia en poblaciones silvestres pequeñas es menos entendida. A mediados de la década de los 80, pequeños números de Takahe no volador (*Porphyrio hochstetteri*) se traslocaron con éxito de la última población remanente en la región montañosa de Fiordland a cuatro refugios insulares. Investigación previa ha mostrado que los Takahe introducidos a islas ponen significativamente más huevos infértiles y crían menos juveniles por huevo que los Takahe en su hábitat nativo en Fiordland. Mostramos por primera vez que la población remanente de Takahe en Fiordland probablemente era severamente endogámica. De ahí postulamos que la mayor endogamia reciente (con base en datos de pedigrí de cuatro generaciones) de Takahe en islas tuvo consecuencias insignificantes sobre la adaptabilidad. Esta hipótesis solo fue parcialmente sustentada. Desde 1991 la eclosión promedio y el éxito de volantones ha permanecido consistentemente bajo (<40% y 77% respectivamente) y no se correlacionó con el rápido aumento del coeficiente de endogamia promedio en Takahe insulares. Ni el coeficiente de endogamia de la descendencia de una pareja ni el estatus de endogamia del macho reproductivo tuvo un efecto significativo sobre el éxito de eclosión o de volantones. Asimismo, el estatus de endogamia de la hembra afectó negativamente el éxito de los volantones. Desconocemos la razón por la cual el bajo éxito reproductivo se exacerbó por la endogamia en hembras pero no en machos ni en parejas; aunque se ha reportado un patrón similar en una población insular de gorriones (*Melospiza melodia*). Suponemos que el éxito reproductivo generalmente menor que exhiben la mayoría de los Takahe*

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insulares es resultado de la depresión endogámica dependiente del ambiente. Concluimos de nuestro análisis de pedigrí que los Takahe insulares están experimentando mayor depresión endogámica, pero la reducción de adaptabilidad parece expresarse únicamente en hembras endogámicas.

Introduction

Inbreeding is of concern to conservation biologists because of its potential adverse effects on fitness-related traits (i.e., inbreeding depression), especially for individuals in small, isolated populations (Frankham 1995*a*). Such effects have been well documented in captive populations (Ralls et al. 1988), and although it has been questioned in the past (e.g., Caro & Laurenson 1994; Caughley 1994), conservation biologists generally accept the potential for inbreeding effects in wild populations (Crnokrak & Roff 1999; Allendorf & Ryman 2002; Keller & Waller 2002). However, the magnitude of these effects and the conditions under which they are expressed vary considerably; thus, more empirical data on inbreeding in the wild has been called for (Keller & Waller 2002).

In New Zealand, which has one of the highest ratios of endangered birds for its land mass (Bell 1991), inbreeding in small, isolated populations on the mainland or on offshore islands is thought to be common, but there is little evidence of inbreeding depression (Craig 1991). This may be because there are few if any comparisons between inbred and outbred populations of the same species or between related and unrelated breeders within the same population (Wallis 1994). Nevertheless, small relict populations that have gone through severe bottlenecks and are known to be highly inbred, such as the Chatham Island Black Robin (*Petroica traversi*), show few signs of inbreeding depression (Ardern & Lambert 1997).

The most frequently used explanation for the persistence of small, isolated populations such as those of New Zealand's endangered birds is that a long history of inbreeding can reduce or eliminate inbreeding depression by "purging" deleterious recessive alleles (Templeton & Read 1984; Hedrick 1994). However, analysis of 25 captive mammal populations indicates that ancestral inbreeding is consistently but only weakly effective in reducing inbreeding depression across a wide variety of taxa (Ballou 1997). More recent research also indicates that purging might be effective in reducing inbreeding depression only if the environmental conditions experienced during the bottleneck prevail. If conditions change or deteriorate, then the additional genetic load can be exposed with a concomitant fitness decrease (Bijlsma et al. 1999). This is known as environment-dependent inbreeding depression. In the case of New Zealand's endangered birds, most are either living in remnant native habitat on the mainland or have been translocated to a similar habitat type on islands from which introduced mammalian predators have been eradicated. In the absence of introduced predators, these populations normally prosper and, as mentioned above, there is little evidence of inbreeding depression (Craig 1991).

An exception to this pattern is the Takahe (*Porphyrio hochstetteri* [formerly *mantelli*] Trewick 1996), a large, flightless, herbivorous rail. Subfossil evidence indicates that Takahe were once widespread throughout New Zealand, although they were never abundant in any one area (Beauchamp & Worthy 1988; Trewick & Worthy 2001). Their numbers declined dramatically after the arrival of Polynesian Maori 1000 years ago, and Takahe were rare and restricted to the Fiordland area of the South Island by the time of European colonization in the 1800s (Beauchamp & Worthy 1988). The last bird was recorded outside the alpine region of Fiordland in 1898, and Takahe were subsequently presumed to be extinct until 1948, when a small remnant population of approximately 250 birds was discovered in the remote Murchison Mountains (50,000 ha), Fiordland (Fig. 1) (Reid
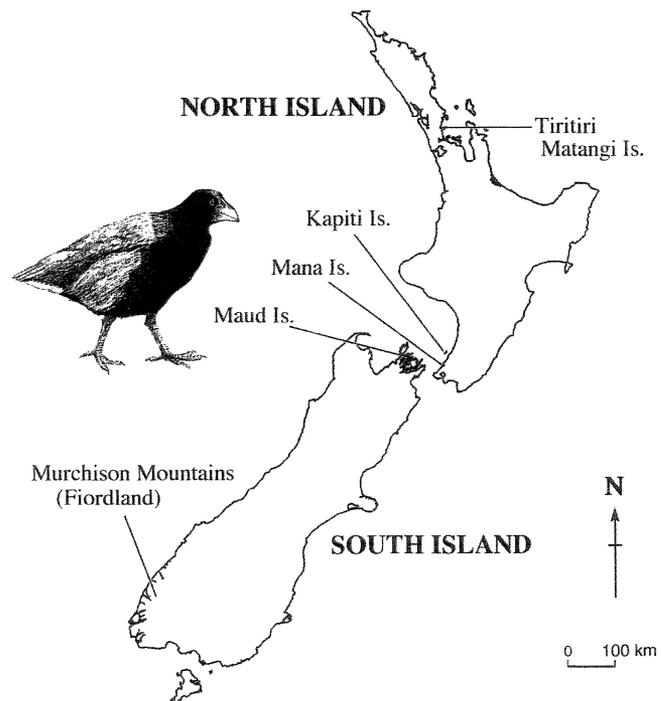

Figure 1. North and South Islands of New Zealand. Location of the last remaining natural population of (Fiordland) Takahe in the Murchison Mountains, with the four translocated island populations marked.

1974; Balance 2001). Takahe are thought to have persisted in mountainous Fiordland because of the area's remoteness from activities associated with human colonization, such as hunting and the introduction of mammalian predators (Bunin & Jamieson 1995). The climate is harsh, however, and the habitat itself is not thought to be optimal for Takahe (Gray & Craig 1991). Although Takahe have been protected since their rediscovery, the decline of the Fiordland population continued until the early 1980s, when numbers remained low but stabilized with the reduction and control of introduced deer, a major food competitor for alpine tussock grasses (Maxwell 2001).

As part of an overall management plan, small numbers of Takahe were introduced to four mammal-free islands in the central and northern parts of New Zealand (Fig. 1) during the mid- to late 1980s and early 1990s (Bunin & Jamieson 1995). Parts of these islands had been farmed in the past and now consist of a mixture of pasture grasses and regenerating native forest. The introduced Takahe experienced high survival success relative to the Fiordland birds, appeared healthy, and nested successfully (Ryan & Jamieson 1998). However, translocated Takahe laid significantly more infertile eggs and raised fewer juveniles per egg than pairs left in their native Fiordland habitat (Bunin et al. 1997; Jamieson & Ryan 2000). Environmental factors that might be peculiar to the islands, such as dietary deficiencies or plant toxins, and that might contribute directly to poor reproductive success have not been detected (Jamieson & Ryan 1999; Jamieson & Easton 2002; I.G.J., unpublished data).

Jamieson and Ryan (2000) analyzed breeding records from 1991 to 1997 and found no correlation between egg infertility and the relatedness of pairs breeding on the islands. Their focus on egg infertility as a measure of reproductive success, however, may have led to an underestimation of the effects of subsequent inbreeding on fitness because other studies have shown that later stages of the life cycle, especially hatching success, can be affected by inbreeding (e.g., Keller 1998). In addition, Jamieson and Ryan's analysis only examined the relatedness of breeding pairs and not paternal and maternal inbreeding and whether this affected reproductive success.

We provide a more extensive analysis, specifically to test for correlation among individual and pair inbreeding coefficients and egg hatching and fledging success for all island-translocated founders and their descendants over the past 14 years (1986–1999). We first show that Takahe are likely to have already been highly inbred in their native habitat prior to their translocation, and then, based on this, hypothesize that further recent inbreeding on the islands should have relatively few or undetectable fitness consequences. We discuss our results in the light of inbreeding effects on other insular populations of birds, and we discuss how loss of genetic variation might be mediated in small, translocated populations of endangered species.

History of Island Transfers

A summary of the timing of founding events for each of the four islands and the number of birds involved is provided in Table 1 (see also Fig. 1). Some of the original founders plus many island-raised birds were subsequently transferred between islands. Indeed, Takahe on all four islands have tended to be managed as a single genetic population. For example, Department of Conservation managers have frequently transferred yearling and adult Takahe between islands to avoid close inbreeding, particularly when only close kin were available as potential mates. From 17% to 29% of the breeders on any one island has originated from the other three islands. Therefore the high rates of human-assisted "dispersal" between the islands indicates that island Takahe should be thought of as consisting of one rather than four isolated populations, although possible island effects have been taken into account in the statistical analysis below.

Of the 25 Takahe originally translocated to the islands, 22 bred at least once (i.e., nested and produced one or more eggs). In addition, up to four generations of island-raised birds (46 birds in total) have also attempted breeding. Previous analysis found no significant effects of year, island, or rearing environment (i.e., initially captive-raised vs. wild-reared) on reproductive success and showed no pattern of improvement over time (Bunin et al. 1997; Jamieson & Ryan 2000).

Table 1. Transfers of founding Takahe (i.e., a bird that is still alive or has living descendents) from the source population in Fiordland to each of the four islands between 1984 and 1999.

Island	Year	Number of Fiordland founders[a] (males:females)
Maud	1984	4 (2:2)
	1985	1 (0:1)
	1989	2 (2:0)
total		7 (4:3)
Mana	1987	2 (1:1)
	1991	2 (0:2)
	1992	1 (1:0)
total		5 (2:3)
Kapiti	1989	4 (2:2)
	1994	1 (1:0)
	1999	1 (1:0)
total		6 (4:2)
Tiritiri Matangi	1991	2 (1:1)[b]
	1994	3 (1:2)
total		3 (1:2)

[a] *Each individual founder is counted only once. For those that were transferred between islands, the founder is associated with the island where it produced the most descendents.*
[b] *Both birds were offspring of founders on Maud.*

Methods

Analysis of Reproductive Success

Island Takahe typically start breeding at 2 years, are generally long-lived (>12 years), and have long-term pair bonds and low reproductive rates. There is no evidence of intraspecific brood parasitism (i.e., egg dumping) in Takahe, and a DNA profiling study revealed no evidence of extra-pair paternity in 27 of 37 offspring for which paternity could be confidently assigned. Paternity of the remaining 10 offspring could not be resolved because of low levels of minisatellite variation, but in none was the resident male excluded (Lettink et al. 2002). This genetic evidence, along with behavioral and life-history data (Lettink et al. 2002), suggests that extra-pair fertilizations are rare or absent in Takahe; thus, we considered the pedigrees we analyzed to be accurate.

Takahe normally produce a clutch of two eggs. In a single breeding season, a pair of Takahe can produce up to two replacement clutches if earlier clutches fail, but pairs rarely fledge more than one chick. Therefore, almost all of the variation in reproductive success among pairs within and between seasons is in the proportion of total eggs laid that hatch and the proportion of hatched eggs that fledge. Many of the second- and third-generation island breeders are still alive, so reasonable estimates of annual survival and lifetime reproductive success are not yet available.

On each island, nests of all breeders were located and inspected several times over the incubation period, during which eggs were candled and eggs that showed no signs of development were removed and opened to determine their fertility status. We checked nest contents at the end of the incubation period to record how many eggs hatched, we visited territories at least every 2 weeks to monitor chick survival. Chicks that survived 8 or more weeks were considered fledged and are referred to as juveniles. All surviving juveniles were color-banded at approximately 4–6 months of age. Because Takahe on islands constitute closed populations, which are intensely monitored, our analysis includes data obtained from all active breeders.

Inbreeding Estimates

The level of inbreeding in a population is typically measured by the calculation of *f*, the coefficient of inbreeding, which represents the probability that two alleles at a locus in an individual are identical by descent (Wright 1977). We calculated *f* for the prospective progeny of all breeding pairs and for individual females and males of each breeding pair with the software program Sparks (International Species Information System 1994). Pedigrees were constructed from observations of territory

establishment, pair bonding, and nest attendance made by staff of the Department of Conservation. Although Takahe normally breed as pairs, 5 of the 57 territories in the data set had an additional male or female breeder (one territory had two males and two females) for which paternity and maternity were likely to be shared. To calculate inbreeding coefficients where at least one male and one female were related, we derived average values from all possible breeding combinations. Excluding these cobreeding groups from the analysis did not change our results, so we left them in the data set. For simplicity, we continue to refer to members of all breeding territories as "pairs."

Pairs were considered related (and thus $f > 0$) if they shared a common ancestor based on pedigree information, and an individual male or female breeder was considered inbred if its parents were related. Pairs that did not share a common detectable ancestor ("unrelated" pairs) were given an inbreeding coefficient of zero. These estimates of inbreeding are minimal because the likelihood of detecting a common ancestor depends on the depth of the pedigree (Keller 1998). We can trace the pedigree of all island-founding birds back to parents or grandparents that came from individual breeding territories scattered throughout the Murchison Mountains (Department of Conservation database, Te Anau). We assumed that descendents originating from different territories in the Murchison Mountains were unrelated, which allowed us to derive a minimum estimate of inbreeding that has occurred since Takahe commenced breeding on the islands. For the majority of island Takahe in the database (75%, $n = 64$), pedigrees extend to at least four grandparents, and many go back three to four generations. Excluding the minority of individuals for which only parents were known (i.e., those with shallow pedigrees) from the analysis did not change our results.

Statistical Analysis

Because of the restricted range of potential values of reproductive outcomes for breeding pairs within a season and the large number of zero values, the proportion (p) of eggs that hatched and the proportion of hatched eggs that fledged were calculated from a pair's combined total of eggs laid and of chicks hatched across years. For the analyses, values of p were transformed:

$$p' = 1/2 \left[\arcsin \sqrt{(X/n + 1)} + \arcsin \sqrt{(X + 1/n + 1)} \right],$$

where X/n is the actual proportion (Zar 1996). Each breeding pair therefore had one (transformed) value for hatching success and for fledging success. If individual male or female breeders bred in more than one pair combination, their reproductive measures were averaged across pairs.

Preliminary analyses indicated no effect of breeding experience on hatching and fledging success. We then looked for an effect of inbreeding through an analysis of variance; the four islands (island), whether or not the breeding male of the pair was inbred (ib-male), and whether or not the female of the pair was inbred (ib-female), were fixed factors in the analysis, and the inbreeding coefficient of the pair's offspring (*f*-pair) was a covariate. In only three pairs were both the male and the female inbred, and because this factor showed no significant effect when included in the initial analysis, it was removed from subsequent analyses. Analyses were rerun with nonsignificant interaction terms removed. We used the general linear model function in Minitab 8.0 (Minitab 1991) to run the analyses.

We also analyzed the data set by dividing birds into related and unrelated pairs and inbred and noninbred males/females and compared their mean differences in hatching and fledging success with *t* tests and 95% confidence intervals. Categorizing pairs as either closely related (offspring's $f = 0.125$) or not closely related ($f < 0.125$) did not change the results, and because sample sizes for inbred males and inbred females were too small to subdivide any further, we present the results for related/inbred ($f > 0$) and unrelated/noninbred ($f = 0$) pairs/males/females only. All values are expressed in means ± SE.

Results

Level of Inbreeding in Island Takahe Relative to the Source Population

The degree of relatedness among Takahe in the Fiordland population is generally unknown, so we estimated the coefficient of inbreeding (*f*) for the source population in 1984, when the first Takahe were translocated to islands, with the following equation,

$$f_t = 1 - (1 - 1/2\,N_e)^t\,(1 - f_0),$$

where f_t is the inbreeding coefficient after *t* generations, N_e is the effective population size during the period of population decline, and f_0 is the initial coefficient of inbreeding before the onset of the decline. Based on Maxwell's estimates (personal communication), we assumed that the Takahe population in Fiordland 100 years earlier was approximately 300 birds, declined to 250 by 1950 and then to 120 by 1965, when it stabilized. To derive a conservative estimate of *f*, we used 0.4 for the ratio of effective population size to census size (for a long-lived, monogamous bird; Frankham 1995*b*), 10 years for average lifespan in the wild (used to calculate generation time), and 0 for the initial inbreeding coefficient. From these values we would expect the present

population in Fiordland to have a minimum inbreeding coefficient of 0.049.

This value is higher than those found for several small island populations of birds (Keller 1998), and any value above 0.025 is considered high for a natural population (Caughley 1994). Therefore, it is highly likely that the Takahe in Fiordland population are inbred. In addition, low average percent differences in shared bands (APD scores) observed in DNA profiles of Fiordland Takahe and those birds translocated to islands (Lettink et al. 2002) are consistent with the evidence of the Takahe's persistence as a small, isolated population over at least the last 100 years.

Of the 25 birds originally translocated to the islands, only one pair formed between known related birds. That pair (a brother and sister) bred together once and produced a chick. Normally, close kin were transferred to other islands to avoid close inbreeding (see section on history of island transfers), but the small number of founders on each island meant that some inbreeding was inevitable. Once Takahe were established on all four islands and the total number of breeding pairs began to increase (from 1991 onward), the average inbreeding coefficient of breeding pairs also increased from 0.0039 in 1991 to 0.074 in 1999 (Fig. 2), assuming that $f = 0$ at the time introductions were initiated. Taking the mean value as of 1999 (0.074) and adding to it the estimated background level of inbreeding in the Fiordland population at the time the translocations were initiated (0.049), the average inbreeding coefficient of island birds (0.123) is 2.4 times greater than the estimated value for the Murchison Mountains population as of 1999 (0.052). Although the level of inbreeding on the islands has increased relatively rapidly, the estimated background level of the founding breeders would still be considered high for a natural population (Caughley 1994; Keller 1998). Therefore, because Takahe appear to be already severely inbred, we predicted that relatedness between breeding pairs and the inbreeding status of individual male and female breeders (based on pedigree records) are poor predictors of reproductive success in island Takahe.

Inbreeding and Reproductive Success

A total of 57 different island pairs nested and laid at least one egg between 1986 and 1999. In total, 434 eggs were laid, of which only 156 (36%) hatched and 81 (19%) produced independent fledglings. Just over half the pairs (51%) had never had a breeding season in which they successfully fledged an offspring.

Since 1991, when the total number of breeding pairs was eight or more, mean annual hatching and fledging success of island Takahe was consistently low (19–40% and 42–77%, respectively) (Fig. 2) but did not correlate significantly with increasing levels of inbreeding (Spearman's rank correlation; hatching: $r_s = -0.38$, $p > 0.10$;
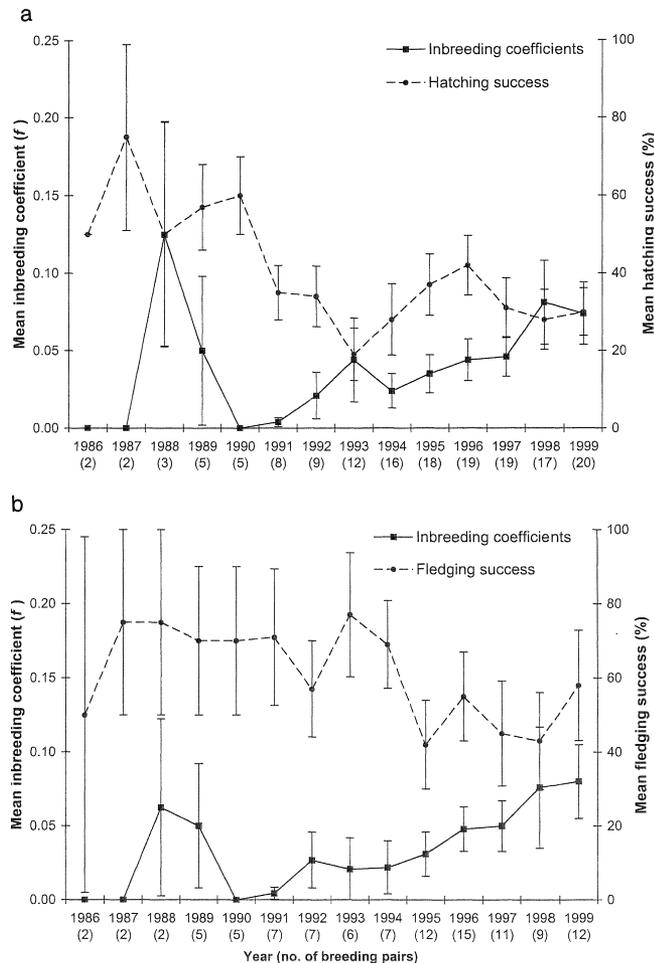
a

b

Figure 2. Relationship between mean inbreeding coefficients and (a) mean hatching success and (b) mean fledging success for breeding pairs of Takahe on four translocated island populations from 1986 to 1999. Number of breeding pairs used to calculate mean hatching success and mean fledging success and their associated mean inbreeding coefficients are shown in parentheses below each year. (By definition, pairs that did not hatch any eggs are excluded from the calculations of fledging success.) Standard error bars are shown above and below means.

fledging: $r_s = -0.61, p > 0.10$). To examine the effects of inbreeding on reproductive success, we included all pairs that laid at least one egg between 1986 and 1999. (Two of these pairs were excluded because breeding records indicated that the male breeders were likely sterile.) Fifty-five pairs were included in the analysis, 30 (55%) of which were related. The relatedness of related pairs ranged from full sibs to half first cousins, but the pedigrees tended to be more complex, with a few pairs sharing more than two common ancestors, resulting in higher inbreeding coefficients of potential offspring (f range: 0.0312–0.344) (Fig. 3). The mean inbreeding co-
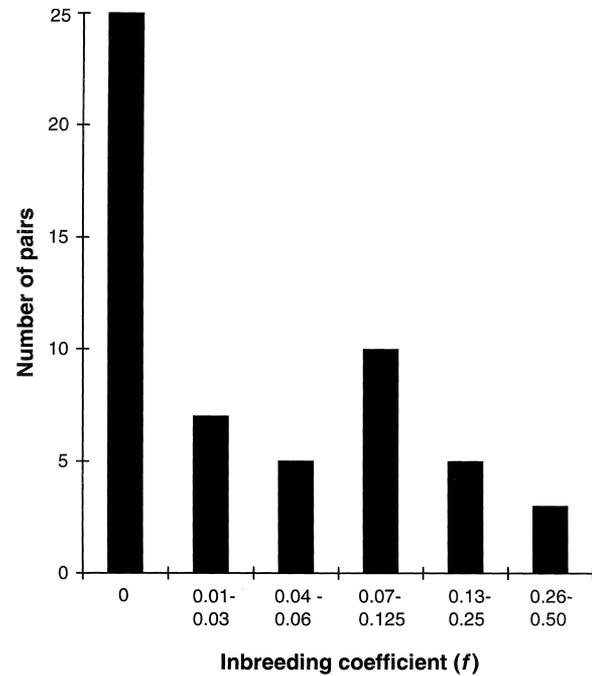

Figure 3. Offspring inbreeding coefficients for 55 breeding pairs of Takahe found on four translocated island populations.

efficient was 0.068 for the 55 breeding pairs used in the analysis, 0.0179 for the 36 male breeders, and 0.0242 for the 28 female breeders.

Neither the fixed factors of "island" or "ib-male" nor the covariate of "f-pair" had a significant effect on a pair's hatching or fledging success (Table 2). The fixed factor "ib-female" also did not significantly affect hatching success, but it did have a significant negative effect on fledging success (Table 2). To see whether inbred females tended to be inexperienced, we reanalyzed fledging success based only on the inbreeding status of the female, the breeding experience of the female (1–2 years, inexperience; ≥ 3 years, experienced), and their interaction as factors. The inbreeding status of the female remained significant ($F_{1,37} = 6.19, p = 0.02$), but neither female breeding experience ($F_{1,37} = 0.54, p = 0.47$) nor the interaction ($F_{1,37} = 0.28, p = 0.60$) were significant.

Similar results were obtained when we compared mean differences in hatching and fledging rates between unrelated pairs ($f = 0$) and related pairs ($f > 0$) and between individual male and female breeders that were either noninbred or inbred (Fig. 4). Only inbred females showed significantly lower fledging success ($t_{18} = 4.28, p = 0.001$). All other comparisons were not significant. Mean fledging success was actually higher for inbred males than for noninbred males, although the 95% confidence interval around the difference in means was large (Fig. 4), presumably because of the small number of inbred males. Sample sizes for inbred females were simi-

Table 2. Results of analysis of covariance with proportion of eggs that hatched and proportion of hatched eggs that fledged as response variables, inbreeding coefficient of the pair (*f*-pair) as a covariate, and island where breeding occurred (island), inbreeding status of the male of the pair (ib-male), and inbreeding status of the female of the pair (ib-female) as fixed factors.*

	Source	F	p
Hatched	island	$F_{3,48} = 0.01$	0.99
	ib-male	$F_{1,48} = 0.22$	0.64
	ib-female	$F_{1,48} = 2.76$	0.10
	f-pair	$F_{1,48} = 0.21$	0.64
Fledged	island	$F_{3,34} = 1.27$	0.30
	ib-male	$F_{1,34} = 0.38$	0.54
	ib-female	$F_{1,34} = 4.92$	0.03
	f-pair	$F_{1,34} = 0.32$	0.58

* All proportional data were transformed (see methods).

larly small. Their 95% confidence interval was smaller (and comparable to those of unrelated/related pairs), however, but was above zero for fledging success only (Fig. 4), indicating that this negative effect on the small number of inbred females was relatively strong. When we regressed the inbreeding coefficients of individual male or female breeders against their mean hatching or fledging success, only *f* values of females and fledging success showed a significant negative relationship ($R^2 = 0.20$, $F_{1,22} = 5.77$, $p = 0.02$).
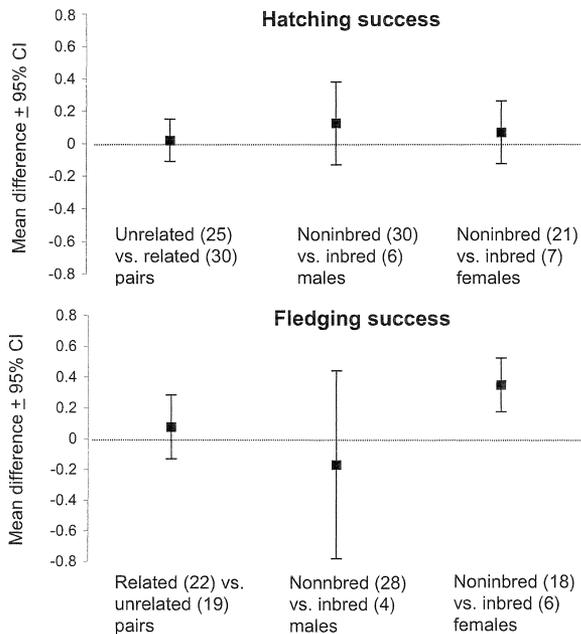

Figure 4. Mean difference ± 95% confidence intervals (CI) in hatching success and fledging success between unrelated and related pairs, noninbred and inbred males, and noninbred and inbred females. Samples sizes are indicated in parentheses. A positive mean difference indicates that the mean value for unrelated, noninbred birds was higher.

We reanalyzed the data set but this time included only those individuals for which all four grandparents were known. This essentially excluded 75% of the founders and decreased the number of breeding pairs to 34. The only substantive difference we found with the earlier analysis was that the negative effect of the factor "ib-female" on fledging success was not quite significant ($F_{1,16} = 3.78$, $p = 0.070$). In the *t* test comparison, however, inbred females still had significantly lower fledging success than noninbred females ($t_{14} = 2.87$, $p < 0.01$). Finally, of the six female founders from which all of the noninbred females descended, five of these also gave rise to inbred females, suggesting that there was no evidence that a few founding individuals were having a large effect on female inbreeding depression.

Discussion

Evidence of a restricted distribution and a small population size indicates that the remnant population of Takahe in the Murchison Mountains is highly inbred. The translocation of small numbers of these inbred Takahe to four "predator-free" offshore island refuges has been successful, in the sense that the founding birds survived and bred successfully and the initial numbers have gradually increased (Jamieson & Ryan 2001). Juvenile recruitment has been much slower than expected, however, because of the high rates of reproductive failure exhibited by most breeding pairs across all four islands and in most years (Bunin et al. 1997; Jamieson & Ryan 2000). The simplest explanation for the reduced reproductive success is that the translocated Takahe have not completely adapted to the island environments. However, no specific environmental variables that can be directly linked to the poor reproductive output of island Takahe have been identified (Jamieson & Ryan 1999; Small 1999; Jamieson & Easton 2002; I.G.J., unpublished data). Furthermore, there is no evidence that hatching or fledging success has improved over the 14 years since Takahe were first established on the islands (Fig. 2), yet the survival of independent juveniles and adults has always been relatively high on the islands (Bunin et al. 1997).

Our preferred explanation is that translocated Takahe are suffering from nonlethal, deleterious inbreeding depression in the form of high egg infertility and low hatching and fledging success. It is possible that island Takahe might be suffering specifically from environment-dependent inbreeding depression (Bijlsma et al. 1999) because they exhibit a much higher level of reproductive failure than inbred Takahe living in their natural habitat in Fiordland (Jamieson & Ryan 2001). Furthermore, small-effect, deleterious alleles might have become fixed in the island populations (which have essentially been managed as a single genetic population) as a result of founder effects and/or drift.

We examined the effects that further, recent inbreeding has had on the reproductive success of island Takahe. We predicted that, because of the previous bottleneck and high levels of inbreeding, the current degree of relatedness of breeding pairs based on pedigree data might be inconsequential to fitness measurements. That is, the pedigree might not reflect the true level of homozygous loci (Bensch et al. 1994). This prediction was supported for fitness estimates for breeding pairs and breeding males but not for females. Low hatching and fledging rates were features of island pairs whether or not members of the pair were related and whether or not the male of the pair was inbred. However, the relatively small proportion of pairs in which the female was inbred had significantly lower fledging success, even lower than the generally low fledging success typical of island Takahe (Bunin et al 1997; Jamieson & Ryan 2000). This result held whether we analyzed the inbreeding status of the breeding female as a fixed factor affecting pairs' fledging success, regressed the f of female breeders against fledging success, or compared mean fledging success of inbred versus noninbred females. The results also held when we restricted our pedigree analysis to only those individuals with at least four known grandparents.

Why poor reproductive success was further exacerbated in inbreeding in females but not in males or pairs is currently unknown, but a similar pattern has been reported in an island population of Song Sparrows (*Melospiza melodia*) (Keller 1998). In other bird studies that have detected inbreeding depression, the relatedness of parents was the main factor leading to reduced reproductive success (e.g., van Noordwijk & Scharloo 1981; Bensch et al. 1994; Kempenaers et al. 1996; Daniels & Walters 2000). Why these differences between species and populations exist is unknown, but they might be related to the fact that the populations of Takahe and Song Sparrows are more insular and have higher background rates of inbreeding. We conclude that inbred island Takahe are undergoing further inbreeding depression, but the reduction in fitness appears to be expressed only in females. It would be informative to compare the fledging success of Fiordland and island females with similar inbreeding coefficients, but sufficient data on the relatedness of individual Fiordland birds are not available.

More generally, translocation of small numbers of individuals from a remnant population to islands where introduced predators have been eradicated can dramatically increase adult survival and juvenile recruitment rates (Armstrong & McLean 1995). Inbreeding may not be problematic in such cases if the translocations are to native habitat similar to the source population. However, inbreeding depression may be more pronounced in endangered species that are moved to habitat that is modified or of poorer quality (Lens et al. 2000). Establishing small populations on several offshore islands has presumably reduced the risk of extinction for Takahe, but may have increased the level of inbreeding. Our results indicate that the management practice of transferring unpaired kin between islands to prevent breeding between close relatives may not have produced the desired effect of improving the reproductive success of island pairs, but it might slow down the rate of increase in the proportion of inbred females in the population.

Lacy (1987) showed that genetic drift is the overriding factor controlling the loss of genetic variation in small populations and that although subdivided populations rapidly lose variability they retain variation across subpopulations better than a panmictic population does. We therefore recommend that the islands with Takahe be managed as a metapopulation, allowing occasional exchanges of birds between islands to minimize close inbreeding, and the periodic introduction of new breeders from the Fiordland population to counteract the effect of drift and increase genetic diversity (Lacy 1987; Craig 1994; Storfer 1999). In addition, pedigree information should be employed in mathematical approaches to gene conservation and founder representation (e.g., Haig et al. 1990) to assist in the planning and design of future translocations of surplus island birds to new island or mainland sites.

Acknowledgments

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