Increased egg infertility associated with translocating inbred takahe (*Porphyrio hochstetteri*) to island refuges in New Zealand

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Abstract

The takahe (*Porphyrio hochstetteri*) is a highly endangered flightless rail, endemic to New Zealand. Since 1984, a total of 24 takahe have been translocated from a small, alpine population of approximately 120 in Fiordland and successfully established on four predator-free lowland islands with introduced pasture grasslands. However, island takahe produce fewer juveniles per egg due to hatching failure being twice as high as it is in the natural population in Fiordland. A comparison among several small, inbred populations of New Zealand birds indicated those that are the result of translocations to new habitat types (takahe and kakapo *Strigops habroptilus*), suffered much higher rates of egg infertility than birds that have remained within their natural habitat range. For takahe, whether breeders had been translocated as juveniles or had been raised on the islands was a poor predictor of reproductive success. The coefficient of inbreeding was high for island takahe but high infertility and low juvenile productivity were features of breeding pairs whether parents were related or not. However, this result might be expected if takahe were already inbred before they were translocated to the islands. If high egg infertility is a consequence of an inbred population being translocated to a new or different habitat, then poor breeding success is something that managers may have to live with in the short term until there is local selection for better breeders. In more general terms, the results of the study have implications for the successful translocation of individuals from inbred populations. © 2000 Elsevier Science Ltd. All rights reserved.

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1. Introduction

The proportion of New Zealand's terrestrial bird species listed as rare or endangered is higher than in any other country and second only to the Hawaiian Islands in terms of relative land area (Halliday, 1978). New Zealand's long history of biogeographical isolation has rendered its endemic species of birds particularly vulnerable to introduced mammalian predators, including humans. Hence, most conservation management effort has focused on either controlling predators on the mainland of New Zealand or establishing small viable populations on predator-free, offshore islands (Bell, 1991; Innes and Hay, 1991).

Factors other than predation, such as inbreeding, are thought to have much less negative impact on endangered species in New Zealand. Many of New Zealand's bird species live in small, isolated populations that have presumably been subjected to a long history of inbreeding, allowing for deleterious recessive alleles to be selected against or purged (Craig, 1991). Assuming these inbred populations continue to be under the same environmental conditions or selection pressures that they experienced in the past, they might not suffer from inbreeding depression (Dhondt, 1996). A recent study of the highly inbred Chatham Island black robin (*Petroica traversi*), which has gone through past and more recent bottlenecks, support this hypothesis (Ardern and Lambert, 1997). Other examples of endangered passerine species being introduced in small numbers on to predator-free island refuges in New Zealand indicates that inbreeding may not be a factor significant to the success of translocations (Craig, 1991). However, the question remains of what would happen if inbred individuals were translocated to an environment or habitat that was substantially different to the one from which they came.

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We examined this question with the endangered takahe (*Porphyrio hochstetteri*) (formerly *mantelli*; Trewick, 1996a, 1997) a large (∼3 kg) flightless gallinule endemic to New Zealand. A single relict population of about 120 individuals inhabits an isolated alpine region of the Murchison Mountains in Fiordland, where numbers appear to be limited by introduced mammalian predators and harsh alpine weather conditions (Bunin and Jamieson, 1995; Maxwell and Jamieson, 1997). Takahe were once distributed widely throughout New Zealand although sub-fossil bones indicate that the form found in the North Island was morphologically and genetically distinct from that in the South Island and they are now considered two separate species (Trewick, 1996a, 1997). Furthermore, molecular evidence indicates that the isolated population of birds remaining in Fiordland is inbred (Lettink, 1999; and see Discussion). However, takahe have persisted in, and presumably adapted to, the alpine-tussock environment (1100–1500 m a.s.l.) of Fiordland over a long period of time (Mills et al., 1984, 1988, 1991), even though this habitat may have been sub-optimal relative to surrounding lowland areas (Gray and Craig, 1991; Jamieson and Ryan, unpublished MS).

Nine juvenile takahe (five males and four females) were translocated to predator-free Maud Island (see Fig. 1) by the New Zealand Wildlife Service (now known as the Department of Conservation) in 1984 and 1985 (Crouchley, 1994). Fifteen additional birds were released on Mana, 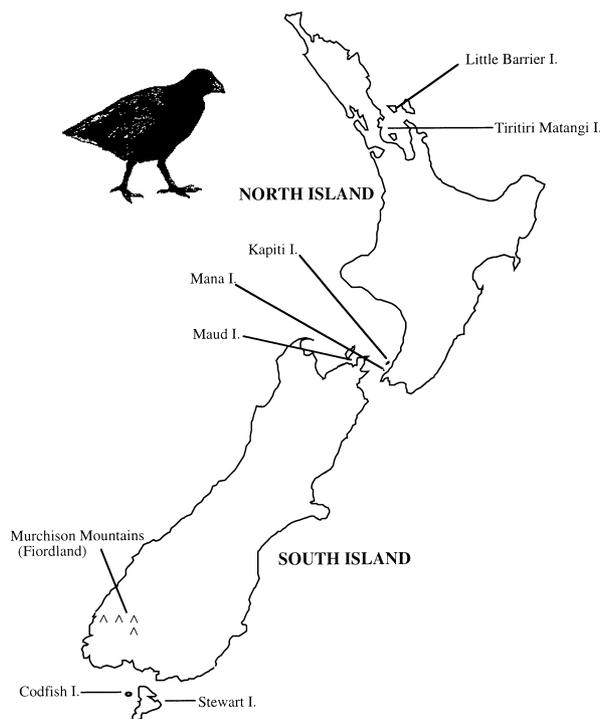Kapiti and Tiritiri Matangi Islands between 1987 and 1993. The first breeding attempt occurred in 1986 (takahe normally start breeding at 2 years of age) and by 1991 there were eight pairs breeding on the four islands. With no predators and a more benign climate, survival of independent juveniles and adult takahe on islands has been high compared to that of the source population in Fiordland (Bunin et al., 1997). Furthermore, translocated birds have bred successfully and raised offspring (Clout and Craig, 1995; Ryan and Jamieson, 1998), and by 1997 there was a total of 19 breeding pairs on the four islands. Thus the translocation of takahe to island refuges could be considered a success story. However, island birds produce significantly fewer juveniles per egg due to hatching failure being twice as high as it is in Fiordland (Bunin et al., 1997). Egg infertility appears to be the main cause of egg failure on islands (Jamieson and Ryan, 1999).

The translocation of takahe onto offshore islands has been uniquely different from the translocation programs for most other species of birds in New Zealand. Small numbers of endangered passerines that have been translocated have been moved from one forest habitat to another of a similar type (Innes and Hay, 1991). Takahe, on the other hand, have come from an alpine-tussock habitat of the Fiordland mountains in the south of the South Island and transferred to lowland islands with introduced grasses and patches of broadleaf forest in the central and northern parts of the country (Fig. 1). Environmental factors that might be peculiar to the islands such as pesticide residues or plant nutrient deficiencies have been examined elsewhere and are not believed to directly contribute to the poor reproductive success of island takahe (Jamieson and Ryan, 1999; and see Discussion). We therefore postulate that the transfer of inbred takahe to habitat substantially different from the one in which they have had a long evolutionary history, may have induced the expression of inbreeding depression (in the form of high egg infertility) in the face of an environmental challenge (Keller et al., 1994).

We cannot test this hypothesis experimentally on takahe as there are restrictions on moving translocated birds back into the natural population because of the risk of introducing disease (Crouchley, 1994). Instead, we compare egg infertility rates of takahe translocated to islands to those of inbred takahe living in their natural habitat on the mainland and to those of other inbred populations of New Zealand birds that have not been translocated. We also compare egg infertility rates and fledging success of takahe pairs that had been originally translocated as juveniles with those raised on the islands, and of island breeders that are related with those that are unrelated, to see if either was a good predictor of reproductive success. Our overall aim is to consider whether the pattern of reproductive failure of island takahe is consistent with a hypothesis of environmentally induced inbreeding depression.

Fig. 1. Map of North and South Island of New Zealand showing natural and translocated populations of takahe and kakapo.

2. Methods

A questionnaire was sent to researchers studying other rare/endangered non-passerine birds in New Zealand which are long-lived and have small clutch sizes (1–3 eggs) similar to that of takahe. Researchers were asked to provide, where possible, data on: (1) proportion of total eggs laid that failed to hatch, and (2) the proportion of failed eggs that were infertile, addled, contained a dead embryo, were predated, or failed for some other reason. Some researchers reported their data on a per year basis while others reported their data as a total over 2 or more years combined.

Addled eggs can result from either infertility or very early embryo death, making it difficult to determine true rates of infertility. In a detailed study of island takahe in 1996 and 1997, eggs were candled earlier than normal in the incubation period and removed from nests to be opened for examination if they showed no sign of development (Jamieson and Ryan, 1999). Close inspection of the germinal disc indicated that all eggs collected at the early stages of incubation were true infertiles (Kosin, 1945). This suggested that the relatively high numbers of addled eggs found in previous years were also likely to be infertile. For the purposes of the comparative analysis and the analysis that follow, addled eggs are included with infertile eggs in all species to give a maximum estimate of infertility.

Although takahe started breeding on the islands in 1986, only two to five pairs bred in the first 5 years and some nest record information was incomplete. Therefore our data analysis begin in 1991 when the number of breeding pairs increased to eight and all nests were monitored on a regular basis by the Department of Conservation. After nests were located each season, eggs at approximately 10 days of age were candled to assess development status, and normally re-candled at least once more before they were due to hatch. When no embryo development was detected, eggs were removed and opened to determine fertility status. The outcome of each egg in a clutch was categorised as either infertile, embryo death, did not hatch (unknown fertility), early chick death (up to 4 weeks), or fledged juveniles (survived at least 4 weeks). Using these data, we examined two components of takahe reproductive success on islands: (1) number of infertile eggs as a proportion of total eggs laid of known fertility per pair per year, and (2) number of fledged juveniles per pair per year. Because first-time breeders tend to lay fewer eggs and have lower reproductive success than more experienced breeders (D. Eason, pers. comm.), they were excluded from the analysis. Experienced breeders normally lay two eggs per clutch and rarely fledge more than one chick. Because these reproductive measures did not conform to normal distributions, we used non-parametric statistical analyses. Means and standard errors are given throughout the paper.

If managers had removed both eggs of a clutch because of lack of development (see above), the nest was normally destroyed to promote re-nesting. In a few cases, the eggs were replaced with dummy eggs (wax-filled) until an egg in the pipping stage was transferred from a pair with two good eggs. This management technique was used to maximise the number of pairs with at least one egg/chick. For the purposes of this analysis, the fates of transferred eggs were still recorded against the parents of the egg.

The mating system of the takahe is presumed to be genetically monogamous and a recent study using multilocus DNA fingerprinting supports this assumption (Lettink, 1999). A 'SPARKS' computer program based on pedigree records was used to generate inbreeding and kinship coefficients for island takahe. If a breeding pair had no detected common ancestors, their offspring were given an inbreeding coefficient of zero and the pair were categorised as unrelated. Although the parents of all the founding birds were known, some pedigrees did not go back further than this and hence inbreeding may be underestimated. Therefore we reanalysed our data using only individuals whose grandparents were known. In calculating a mean kinship coefficient for all breeding pairs we treated the four islands as one population because of the substantial number of inter-island transfers during the course of the study (see below).

When the island populations were first being established, yearling and adult takahe were regularly transferred (up until 1995) from one island to another to either increase the number of breeding pairs, to equalise the sex ratio of unpaired birds, or to avoid close inbreeding (particularly when only close kin were available as potential mates). Hence, the overall degree of inbreeding on any particular island is potentially lower than it would have been if the islands had not been actively managed in this manner, although some inbreeding still occurred (see Results). The number of birds on the islands is still increasing and Maud, Mana and Tiritiri Matangi Islands have reached less than 50% of their estimated carry capacity (Ryan and Jamieson, 1998). Kapiti Island, which has the smallest amount of suitable habitat, is close to its carrying capacity of five pairs.

3. Results

3.1. Comparison of egg failure rates in takahe and other New Zealand birds

The percentage of total eggs that failed to hatch was high for most of this sample of rare/endangered birds in New Zealand with the exception of yellow-eyed penguins (*Megadyptes antipodes*) in Otago (Table 1). However, the percentage of total eggs that were infertile was

Table 1
Egg infertility and other causes of reproductive failure in several populations of endangered species in New Zealand

Species (modal clutch size)	Population	Total no. of eggs laid	Failed eggs (% total eggs laid)	Infertile eggs (% total eggs laid)	Infertile eggs (% failed eggs)	Embryo deaths (% failed eggs)	Predation (% failed eggs)	Other[a] (% failed eggs)	Source
Takahe (2) (Porphyrio mantelli)	Fiordland[b,c]	61	31	19	60	22	1	17	D. Eason, unpubl. data
Kakapo (3) (Strigops habroptilus)	Islands[c]	45	66	42	64	24	0	13	I. Jamieson, unpubl. data
	Codfish Is.[d]	36	47	27	58	25	17	0	D. Merton, unpubl. data
New Zealand pigeon (1) (Hemiphaga novaseelandiae)	Little Barrier Is.[d]	10	70	62	89	11	0	0	D. Merton, unpubl. data
	Pelorus Bridge[e]	45	67	4	7	0	33	60	Clout et al., 1995
Brown kiwi (1) (Apteryx australis)	Tangiteroria[e]	26	77	15	20	0	10	70	Porter, 1989
Great spotted kiwi (1) (Apteryx haastii)	Northwest Nelson[e]	19	63	16	25	0	17	58	McLennan et al., 1996
Yellow-eyed penguin (2) (Megadyptes antipodes)	Otago[c]	104	15	14	89	0	0	11[f]	Darby and Sneddon, 1990

[a] Includes broken, disappeared, displaced and desertion (which can be a consequence of predation events).
[b] Excludes eggs that were reared under artificial conditions.
[c] Data are averages derived from several breeding seasons.
[d] Data from individual female kakapo were averaged across two or more breeding seasons.
[e] Data are totals from several breeding seasons combined.
[f] Recorded as missing but may have been due to predation.

higher in island takahe (42%) and in kakapo on Little Barrier Island (62%) compared to their sister populations (19 and 27%, respectively), as well as other populations of endangered species throughout New Zealand (Table 1). Differences in the way proportional data were reported and summarised (see Methods and Table 1) precluded the different species from being compared statistically.

A high percentage of the failed eggs of yellow-eyed penguin were categorised as infertile (89%), but this represents only a small proportion of the total eggs laid (Table 1). Similarly, the high percentage of failed eggs that were infertile in Fiordland takahe and Codfish Island kakapo represented a smaller proportion of the total eggs laid than was the case for island takahe or Little Barrier Island kakapo (Table 1). In addition, egg infertility appears to be a greater problem than embryo death in takahe and kakapo. In both species of kiwi, egg failure is primarily due to desertion. Desertion is a consequence of disturbance by predators or researchers although a small (unspecified) number of 'rotten' eggs were deserted late in the incubation stage and may have been infertile (McLennan et al., 1996).

3.2. Infertility and juvenile production in island takahe

Infertility and juvenile productivity data from 26 males and 25 females in 34 pairings and 101 pair-years between 1991 and 1997 were analysed for island takahe. There were no significant differences in the proportion of infertile eggs or the number of juveniles produced across the four islands (Kruskal–Wallis tests, $H = 1.6$ and 0.30, $P = 0.66$ and 0.96, respectively). There were also no significant differences in the proportion of infertile eggs or the number of juveniles produced across the seven years of the analysis (Kruskal–Wallis tests, $H = 4.7$ and 4.2, $P = 0.59$ and 0.65, respectively).

We first asked whether breeding birds that originally hatched and were raised on the islands ($n = 20$ pairs) had better reproductive success than birds that were originally translocated to the islands ($n = 12$ pairs). There was no significant difference between island raised and translocated birds in either the proportion of infertile eggs (0.48 ± 0.08 versus 0.50 ± 0.08) or in the number of juveniles produced (0.36 ± 0.11 versus 0.53 ± 0.14) (Mann–Whitney tests, $W = 269.5$ and 308.5, P values = 0.94 and 0.38, respectively).

With the small number of founder birds, it is not surprising that island takahe have a relatively high average coefficient of inbreeding, whether the analysis includes all pairs ($f = 0.049$, $n = 37$) or only pairs with known grandparents ($f = 0.067$, $n = 27$). The mean annual coefficient of inbreeding increased initially after 1991 and has fluctuated between 0.030 and 0.060 since 1993 (Fig. 2). Forty-three percent of all pairings ($n = 37$; includes first-time breeders) were between related birds,
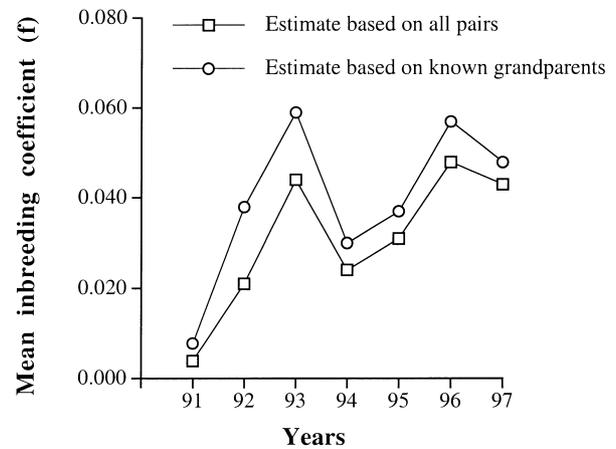

Fig. 2. Mean coefficients of inbreeding for island takahe for the analysis period (1991–1997). Mean inbreeding was calculated from the inbreeding coefficients of all breeding pairs and all breeding pairs with known grandparents in any particular year.

which increases to 59% ($n = 27$) if only pairs for which all grandparents are known are included. However, there was no significant difference between 14 related pairs and 22 unrelated pairs in the mean proportion of infertile eggs laid (0.54 ± 0.084 and 0.50 ± 0.074, respectively) (Mann–Whitney test, $W = 390.5$, $P = 0.60$) or in the mean number of juveniles raised (0.36 ± 0.14 and 0.44 ± 0.10, respectively) ($W = 419.5$, $P = 0.67$). These results did not change if only those individuals whose grandparents were known were included in the analysis ($P = 0.68$ and 0.95, respectively). Therefore, high infertility and low juvenile productivity were features of takahe pairs in translocated populations whether breeders were related or not. There was a trend for inbred female breeders ($n = 3$) to have higher infertility (0.69 ± 0.23 versus 0.44 ± 0.069) and lower juvenile productivity (0.17 ± 0.17 versus 0.48 ± 0.13) than female breeders that were not inbred ($n = 11$), but the number of inbred breeders (with known grandparents) was small and the pattern not statistically significant ($W = 75.5$, $P = 0.31$ and $W = 89.0$, $P = 0.34$, respectively). There was no such trend between 2 inbred males and 10 males that were not inbred (infertility: 0.43 ± 0.18 and 0.54 ± 0.096; number of juveniles: 0.75 ± 0.25 and 0.48 ± 0.18) ($W = 68.5$, $P = 0.52$ and $W = 62.0$, $P = 0.57$).

The only significant pattern uncovered in our analysis was that high infertility and low juvenile productivity were more evident in first clutches of the season than in second or third clutches. Only 24% ($n = 54$) of the total number of juveniles produced between 1991 and 1997 came from the 165 first clutch eggs, while 57% of juveniles came from 116 second clutch eggs and 19% of juveniles came from 33 third clutch eggs. Comparisons within years indicates that significantly more juveniles per egg came from second clutches (0.25 ± 0.029) than from first clutches (0.08 ± 0.019) (Wilcoxon paired-sample test, $T^+ = 28$, $n = 7$ years, $P = 0.02$). On an individual

basis, 17 males (65%) and 16 females (64%) have never produced a juvenile from a first clutch. A high proportion of eggs in first clutches were infertile (53.6% ± 4.57, $n = 7$ years) or the embryos/chicks died during incubation or just after hatching (38.0% ± 3.61). These proportions were lower, on average, for second clutches (42.7% ± 5.20 and 33.1% ± 4.61, respectively), although they were not significantly different when compared within years (Wilcoxon paired-sample test, $T^+ = 22$, $n = 7$, $P = 0.22$ for infertility and $T^+ = 19$, $n = 7$, $P = 0.46$ for embryo/chick death).

Island females are laying their first clutches 2 months earlier on average (September–October) than Fiordland female takahe (November–December). It is therefore possible that island males are not producing adequate numbers of sperm or females are producing poor quality eggs early in the season, resulting in higher rates of infertility. We tested this by seeing if there was a relationship between date of laying and the proportion of infertile eggs in the last three years of the study. The relationship was negative (i.e. more infertility early in season) in two of the years (Spearman's Rank Correlation, 1997: $r_s = -0.40$, $n = 14$, $P = 0.14$, 1995: $r_s = -0.33$, $n = 12$ $P = 0.25$), positive in the other (1996: $r_s = 0.34$, $n = 15$, $P = 0.20$), and in none of the years were the relationships significant. From these results, we conclude that fertility rates appear to improve with re-nesting and laying of a second clutch, but not with laying date per se.

4. Discussion

Unlike many translocation experiments reported in the literature, the transfer of takahe and kakapo to island refuges in New Zealand has been relatively successful, with high rates of adult survival and frequent breeding attempts (Clout and Craig, 1995). However, egg infertility rates of takahe on islands and of kakapo on Little Barrier Island were very high relative to Northern Hemisphere birds (see Koenig, 1982), and also high relative to other small and likely inbred populations of New Zealand birds which have remained in their natural habitat (Table 1).

The kakapo population on Little Barrier Island has gone through a similar translocation process to that of takahe on islands. A remnant population of kakapo occurred on Stewart Island in the far south of the South Island of New Zealand (see Fig. 1). Because Stewart Island had feral cats, most of the remaining kakapo (approximately 40 adults) were transferred either to nearby Codfish Island, which was similar in habitat and climate to Stewart Island, or to Little Barrier Island, a semi-tropical island off the north eastern coast of the North Island (Moorhouse and Powlesland, 1991; Clout and Merton, 1998). As with takahe, translocated adult

kakapo have had very high survival rates and have bred on both islands (Clout and Craig, 1995; Clout and Merton, 1998). However, our analysis showed that infertility was relatively high for kakapo translocated to Little Barrier Island compared to those birds moved to nearby Codfish Island, suggesting that infertility may be related to transferring birds to substantially different habitat type rather than the translocations per se.

High egg infertility and poor fledging success in island takahe could be directly due to environmental factors such as presence of pesticides or deficiencies in trace elements in island food-plants. Our related research has found no evidence in support of this except a non-significant trend for manganese, an essential trace element important in avian egg fertility and hatching success, to be in lower concentrations in island than in Fiordland takahe (Jamieson and Ryan, 1999). However, the increase in egg fertility and fledging success associated with laying second and third clutches, which are presumably energetically demanding, would not be expected if essential nutrients were deficient. In addition, a sister species to the takahe, the pukeko (*Porphyrio porphyrio*), which has been self-introduced on islands where takahe occur and lives in the same habitat and feeds on the same plant species (Trewick, 1996b), has relatively low rates of egg infertility and high juvenile production (Jamieson and Ryan, 1999). These results taken together, along with the high adult survival, do not support the notion that island habitat is of poor quality.

It is possible that male and female reproductive systems of island takahe are not synchronised for first clutches of the season but become so after one nesting attempt. However, why this should be the case (i.e. why females are ready to lay eggs but males are not ready to produce sperm) is not at all clear and would be unexpected. Attempts to analyse sperm quantity by examining the perivitelline membrane of infertile eggs failed because sperm can no longer be detected on the membrane once eggs have been incubated for 7 days or longer-the minimal period for which fertilisation of takahe eggs can be detected by candling (Small et al., unpublished).

A more likely reason for the differences in fertility rates between clutches is that reproductive success improves with reduced inter-territorial aggression as the breeding season progresses. Density of territorial birds on islands is higher than in Fiordland (J. Maxwell, pers. comm.) and island managers have witnessed intense fighting early in the breeding season associated with take-overs of territories or mates. However, only small numbers of island pairs are involved in fights in any one year, and fertility rates and fledging success are relatively low even in second or third clutches of the season. Therefore high levels of territorial aggression do not completely explain the much lower reproductive success of island takahe, but it may be a contributing factor.

We believe that the poor reproductive success of island takahe (and that of kakapo on Little Barrier Island) is best interpreted as the result of environmental and genetic factors interacting, that is, high egg infertility may in part be due to inbreeding depression associated with a substantial change in habitat. The mean inbreeding coefficient for island takahe was high relative to other insular populations of birds where inbreeding coefficients have been estimated (see Keller, 1998). This is presumably due to the small number of founding birds transferred to the islands and the subsequent high proportion of pairings between related birds. Although breeding pairs that were unrelated had just as high infertility rates as breeders that were related, this result would be expected if the source population and founding birds were already inbred from previous bottlenecks so that the proportion of homozygous loci is similar between paired birds that are related and unrelated (Bensch et al., 1994). Recent molecular evidence supports this interpretation for takahe. Mean band sharing values of 0.57 obtained from a sample of the original founding birds and 0.66 for unrelated island takahe (Lettink, 1999), fall above the value of 0.51 which is indicative of an inbred population (Papangelou et al., 1998).

Studies have indicated that inbred populations can do as well as outbred populations as long as the inbred group is subjected to similar environmental conditions or selection pressures it experienced during the period of the genetic bottleneck. However, when inbred groups are subjected to new environmental stresses, reproductive success and/or survival can decline markedly (e.g. Keller et al., 1994; Miller, 1994; Pray et al., 1994). Other studies further indicate that inbreeding in birds tends to affect fertility more in males than females (i.e. females still lay similar number of eggs), but that inbred females have reduced hatchability of their eggs (Sittmann et al., 1966; Keller, 1998). Takahe exhibit both of these forms of reproductive failure and we speculate that translocating inbred birds to a different environment has exacerbated this problem. We acknowledge that we are unsure what exactly it is about islands that would induce some form of physiological stress in breeding takahe. Although the island environment does not appear to be climatically as harsh as that of Fiordland, both habitats are nevertheless substantially different particularly in their plant-food species and in the density of birds (see above), and one or both of these may be the key.

Finally, the results presented here are not meant to imply that the translocation of takahe to predator-free islands has been a failure, as the overall population has steadily increased despite the poor reproductive success of breeding pairs. Indeed, predator-free island populations have been the major reason why the overall numbers of takahe have increased since 1984 when takahe were first introduced to islands (Jamieson and Ryan, unpublished). In addition, establishing takahe in several small populations outside of Fiordland has substantially reduced the chances of this highly endangered bird going extinct (Craig, 1991, 1993).

Nevertheless, poor reproductive success in the form of high egg infertility and low fledging success is still an anomaly of translocated populations. If our hypothesis that this is due to inbreeding depression is true, then poor breeding success is something that managers may have to live with in the short term until there is local selection for better breeders. Whether birds should continue to be transferred between islands to maximise outbreeding or be allowed to further inbreed within islands to promote locally adaptive gene complexes (Craig, 1991, 1993), is still an issue the Takahe Recovery Group needs to address. In more general terms, the results of this study may have implications for translocations of individuals from inbred populations to habitat considered suitable for survival, but which might be different enough from that of the source population to induce inbreeding depression.

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