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# Inbreeding and Endangered Species Management: Is New Zealand Out of Step with the Rest of the World?

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**Abstract:** *There is growing evidence that inbreeding can negatively affect small, isolated populations. This contrasts with the perception in New Zealand, where it has been claimed that native birds are less affected by inbreeding depression than threatened species from continental regions. It has been argued that New Zealand's terrestrial birds have had a long history of small population size with frequent inbreeding and that this has "purged" deleterious alleles. The rapid recovery of many tiny and inbred populations after introduced predators have been controlled, and without input from more genetically diverse populations, has further supported the view that inbreeding is not a problem. This has led to a general neglect of inbreeding as a factor in recovery programs for highly endangered species such as the Black Robin (*Petroica traversi*) and Kakapo (*Strigops habroptilis*). We examined the reasons for this situation and review the New Zealand evidence for genetic purging. Complete purging of the genetic load and elimination of inbreeding depression are unlikely to occur in natural populations, although partial purging may be more likely where small populations have become inbred over an extended period of time, such as on small isolated islands. Recent molecular data are consistent with the view that island endemics, including New Zealand's threatened birds, have low genetic variation and hence have possibly gone through longer periods of inbreeding than threatened species from continental regions. Nevertheless, results from recent field studies in New Zealand indicate that, despite the opportunity for purging, inbreeding depression is evident in many threatened species. Although inbreeding depression has not prevented some populations from recovering from severe bottlenecks, the long-term consequences of inbreeding and small population size—the loss of genetic variation—are potentially much more insidious. The degrees to which genetic factors reduce population viability generally remain unquantified in New Zealand. Although minimizing ecological risks (e.g., preventing reinvasion of islands by mammalian predators) will continue to receive high priority in New Zealand because of their much larger impacts, we advocate that genetic considerations be better integrated into recovery plans.*

**Key Words:** Black Robin, genetic purging, Kakapo, Takahe

Endogamia y Gestión de Especies en Peligro: ¿Está Nueva Zelanda Desfasada del Resto del Mundo?

**Resumen:** *Cada vez hay más evidencias de que la endogamia puede afectar negativamente a poblaciones pequeñas aisladas. Esto contrasta con la percepción en Nueva Zelanda, donde se ha afirmado que la endogamia tiene menos efecto sobre las aves nativas que sobre las especies amenazadas de regiones continentales. Se ha argumentado que las aves terrestres de Nueva Zelanda tienen una larga historia de poblaciones pequeñas con endogamia frecuente y que esto ha "purgado" alelos deletéreos. La rápida recuperación de muchas poblaciones pequeñas y endogámicas después de que se ha controlado a depredadores introducidos, y sin entradas desde poblaciones más diversas genéticamente, ha reforzado la idea de que la endogamia no es un problema. Esto ha llevado a la desatención general de la endogamia como un factor en los programas de recuperación de especies en peligro crítico como *Petroica traversa* y *Strigops habroptilis*. Examinamos las razones de esta situación y revisamos la evidencia de purga genética en Nueva Zelanda. Es poco probable que haya una purga completa de la carga genética y eliminación de la endogamia en poblaciones naturales, aunque*

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es más probable que haya purgas parciales donde las poblaciones han sido endogámicas durante extensos períodos de tiempo, tal como en pequeñas islas aisladas. Datos moleculares recientes son consistentes con la idea de que especies endémicas a islas, incluyendo las especies de aves amenazadas de Nueva Zelanda, tienen variación genética baja y por lo tanto es posible que hayan tenido períodos de endogamia más prolongados que los de especies de regiones continentales. Sin embargo, los resultados de estudios de campo recientes en Nueva Zelanda indican que, a pesar de la oportunidad de purga, la endogamia es evidente en muchas especies amenazadas. Aunque la endogamia no ha impedido que algunas especies se recuperen de cuellos de botella severos, las consecuencias a largo plazo de la endogamia y del tamaño poblacional pequeño - la pérdida de variación genética - son potencialmente más insidiosas. El grado en que los factores genéticos reducen la viabilidad poblacional en general no está cuantificado en Nueva Zelanda. Aunque la minimización de los riesgos ecológicos (e.g., prevenir la reinvasión de mamíferos depredadores en las islas) seguirá teniendo alta prioridad en Nueva Zelanda debido a su mayor impacto, recomendamos que los temas genéticos sean considerados en los planes de recuperación.

**Palabras Clave:** *Petroica traversi*, *Porphyrio mantelli*, purga genética, *Strigops habroptili*

## Introduction

Habitat loss and invasive species are considered the primary drivers of population extinction. There is growing evidence, however, that inbreeding depression can further affect wild populations once they become small (Crnokrak & Roff 1999; Hedrick & Kalinowski 2000; Keller & Waller 2002). Empirical studies have confirmed direct links between inbreeding and/or loss of genetic variation and population viability (e.g., Westemeier et al. 1998; Madsen et al. 1999). In a recent review of the literature, Keller and Waller (2002) concluded that inbreeding and inbreeding depression occur commonly in nature and can be severe enough to affect the viability of small and isolated populations, especially those of endangered species.

The New Zealand avifauna has one of the highest proportions of endangered species for its landmass (Bell 1991), yet only 1 of the 13 bird studies listed by Keller and Waller (2002) as an example of inbreeding depression comes from New Zealand. New Zealand's endangered bird populations have a long history of intensive study (Bell 1991) yet are conspicuous by their absence in the inbreeding literature. If inbreeding depression is important in reducing persistence probability of small populations, we would expect the negative consequences of inbreeding to be evident in New Zealand's well-studied and highly endangered bird fauna. In this essay we explore why New Zealand conservation biologists appear less likely to focus on genetic factors when implementing recovery plans for the country's threatened avifauna.

## Causal Factors of Population Decline in New Zealand

Few would disagree that on an ecological time scale the greatest risks of extinction to small populations come primarily from habitat loss and introduced predators. This is

nowhere more evident than in New Zealand. Hunting and forest burning by early Polynesians eliminated more than 35% of endemic land birds, and further land clearance and widespread introduction of exotic mammals (particularly rats, mustelids, and cats) by Europeans threatened much of the surviving fauna (Duncan & Blackburn 2004). Because the endemic fauna evolved in the absence of terrestrial mammals, the overriding focus for recovery of endangered populations is limiting predation by introduced mammals (Clout 2001). Although many species of endemic birds, frogs, and invertebrates are characterized by low population numbers, range contraction, and severe population fragmentation, reduced genetic variation and inbreeding are often seen as inconsequential when behaviorally naïve endemics are faced with repeated outbreaks of carnivorous rats, stoats, or feral cats. Managers tend to focus efforts on restoration programs that establish small populations on offshore islands free of introduced predators and are less concerned about long-term consequences of inbreeding (Armstrong & McLean 1995).

Although predation by exotic mammals has led to the extinction and fragmentation of many native species, the argument that genetic factors are unimportant relative to introduced predators is misplaced. Inbreeding effects operate on a longer time scale (generations) than ecological effects (years) (Soulé & Mills 1998). Even if conservation measures succeed at controlling direct threats such as introduced predators, inbreeding and loss of genetic variation may ultimately lead to extinction. Therefore genetic factors could be influencing demographic processes affecting population persistence in New Zealand, but they could be less obvious than the effects of habitat destruction and depredation by exotic mammals.

## The Role of Inbreeding in New Zealand Species

By focusing more on the ecological agents of declining populations than on genetic consequences once populations become small (Caughley 1994), conservation

managers in New Zealand are probably no different from managers elsewhere. As far as we are aware, however, only in New Zealand is there a widely held view that threatened bird species are less susceptible to the effects of inbreeding depression than species elsewhere. For example, in a recent review of conservation issues in New Zealand, the effects of inbreeding in small populations warranted only one sentence, "New Zealand's wildlife might be less susceptible to inbreeding depression than species elsewhere" (Craig et al. 2000). This conclusion stems from Craig's (1991, 1994) earlier work, where he questions whether genetic models and associated management guidelines derived for threatened species in continental regions of the Northern Hemisphere apply to species from small, insular populations in places like New Zealand.

Craig's (1991, 1994) main concern is that recommendations for translocating and establishing new bird populations with large numbers of genetically diverse founders (i.e., the so-called  $N_e = 50/500$  rule, Franklin 1980) are based on genetic models that assume natural populations are generally large and outbred. Craig argues that most of New Zealand's land-bird populations, particularly those restricted to the many (>700) offshore islands, are small, isolated, and subject to frequent inbreeding, and have been so for many generations. Furthermore, gene flow among populations has been restricted because many of New Zealand's nonmigratory land birds are flightless or weak flyers and produce offspring that normally settle close to their natal area. Craig (1991, 1994) was not arguing that New Zealand's species are unique, but that they are similar to many island endemics, for which the frequency of inbreeding is expected to be higher than that of species in larger continental populations. In making this distinction between islands and large continental landmasses, Craig's key point is that a population with a history of inbreeding is more likely to have purged deleterious recessive alleles and hence is less likely to exhibit inbreeding depression than an outbred population with a more recent and brief history of inbreeding, an argument which, at the time, gained some acceptance in the conservation literature (Templeton & Read 1984).

Craig (1991, 1994) does not provide any data on inbreeding depression but makes the point that the majority of translocated island populations of native birds originating from relatively small founder numbers thrive in the absence of alien predators, a point that has empirical support (Taylor et al. 2005). Craig therefore questions the perceived wisdom that reintroductions should use hundreds of founders to avoid the short-term negative effects of inbreeding depression (Franklin 1980).

Despite the lack of empirical evidence, Craig's (1991, 1994) arguments appear to have been accepted by many New Zealand conservation biologists and managers, who tend to downplay inbreeding as a potential concern

for the viability of a population. This is most evident in recovery programs for two high-profile species: the Chatham Island Black Robin (*Petroica traversi*) and the Kakapo (*Strigops habroptilis*). Black Robins were once widespread throughout main Chatham Island (90,000 ha) and its associated islets but declined rapidly because of loss of forest habitat and predation by introduced mammals (Butler & Merton 1992). By the 1880s, Black Robins were confined to a 9-ha patch of forest on Little Mangere Island, which would have supported only 20–30 individuals at any one time. By 1976 the population was reduced to 5 individuals (1 breeding female), but it increased to 120 birds over a 20-year period with the onset of intensive management, which included transferring birds to better-quality habitat and cross-fostering eggs to a sister species to increase productivity (Butler & Merton 1992). Hands-on management ceased after 1989, and the population size is currently 200 individuals distributed between two islands (E. Kennedy, personal communication).

Butler and Merton (1992) question whether inbreeding depression or loss of genetic variation prevented Black Robins from recovering, given that many pairs showed high juvenile survival and no "particular vulnerability to disease." The only problem they reported was low hatching success (67%), which was partly associated with some birds laying eggs on the rim of nests. Ardern and Lambert (1997) subsequently found that the level of variation at minisatellite loci in the Black Robin is among the lowest recorded for any avian species in the wild (0.84 band-sharing coefficient). The low variation appears to be due to the Black Robin's persistence as a single, small population for at least the last 100 years, or approximately 25 generations. They suggest that the high survival and reproductive performance indicate that the Black Robin appears to be viable under existing conditions, perhaps owing to a long history of inbreeding and the elimination of deleterious alleles. Ardern and Lambert (1997) conclude that "... intense inbreeding and low levels of genetic variation do not necessarily prohibit the continued survival of endangered species."

Wallis (1994) and Frankham et al. (2002) dispute the above claim, noting that although populations exhibiting inbreeding depression can reach the same population size as noninbred populations, they may take longer to reach the carrying capacity, be more susceptible to new impacts such as introduced diseases or parasites, and be slower to recover from any subsequent population catastrophes. A recent study confirmed that variation at the class II B MHC loci (which play a role in immune function) has been reduced in the Black Robin compared with a nonendangered congener (Miller & Lambert 2004). Although a preliminary survey of the Black Robin population found no evidence of viral, protozoan, or bacterial infections, the population could still be vulnerable to novel infections (Miller & Lambert 2004). Finally, Frankham et al. (2002) argue that using the one surviving population of

Black Robin as evidence of its viability is like pointing to the existence of one 80-year-old smoker as evidence that smoking is harmless.

The Kakapo was once widespread throughout New Zealand, but its range contracted drastically over a 200-year period (Clout & Merton 1998). Except for a single male from Fiordland, the entire extant population comes from Stewart Island. The Stewart Island population continued to decline slowly through predation by feral cats and reached a low of approximately 50 birds in the 1970s, although its lek-mating system means that the effective population size would have been much smaller. Kakapo are long lived (up to 30 years in the wild), do not start breeding until 7 years of age, and thus have a long average generation time (approximately 15 years). Molecular analyses confirm that Stewart Island Kakapo have substantially reduced genetic variation (Robertson et al. 2000; Miller et al. 2003, Table 1), suggesting that they are likely to have been subject to a lengthy period of inbreeding and genetic drift.

When asked about the prognosis for Kakapo, given its tiny population and low genetic diversity, a senior biologist working for the recovery program argued that the Kakapo should be able to cope because many of New Zealand's birds retreated into small refuges during the ice ages and made successful comebacks, whereas others have survived for centuries on small, isolated islands. Furthermore, "[T]he problems associated with such genetic bottlenecks may not be so bad in New Zealand as they are in other places" (Pain 2002).

This line of reasoning follows that of Craig (1991, 1994) and assumes that slow inbreeding followed by genetic purging has occurred historically. The statement that the problems associated with such genetic bottlenecks may not be so bad, however, is debatable. These comments were made in a *New Scientist* article (Pain 2002) following the most successful breeding season (2001–2002) experienced by Kakapo since intensive management began in 1982. This success (24 chicks; more than all previous years combined) was due in no small part to the efforts of

**Table 1.** Levels of microsatellite genetic diversity in threatened bird species categorized as either island endemics (I) or continental species (C) and ranked according to expected heterozygosity ( $H_e$ ) for polymorphic loci; average number of alleles per locus (A) is also reported.<sup>a</sup>

Threatened species (ref. code) <sup>b</sup>	Island or continental	No. of individuals sampled	No. of polymorphic loci	$H_e$	A
Kakapo (1)	I (NZ) <sup>c</sup>	29	0 <sup>d</sup>	0 <sup>d</sup>	1.0 <sup>d</sup>
Mariana Crow (2)	I	16	6	0.24 <sup>e,f</sup>	2.2 <sup>e</sup>
Great Bustard (3)	C	52	6	0.35	4.8
Seychelles Kestrel (4)	I	4	2	0.38 <sup>e</sup>	2.5 <sup>e</sup>
San Clemente Island Loggerhead Shrike (5)	I	26	6	0.40	2.3
Takahe (6)	I (NZ)	68	5	0.42	2.0
Mauritius Kestrel (4)	I	75	3	0.42 <sup>e</sup>	2.3 <sup>e</sup>
Tieke/S.I. Saddleback (7)	I (NZ)	61–122	4	0.45	3.2
South Island Robin (7)	I (NZ)	13–65	6	0.48	4.2
Seychelles Warbler (8)	I	25	30	0.48	2.8
Peregrine Falcon (9)	C	22–28	12	0.49	4.1
Laysan Finch (10)	I	44	9	0.51	3.1
Spanish Imperial Eagle (11)	C	38	18	0.52	4.0
Kokako (12)	I (NZ)	8–24	4	0.56	3.8
Greater Prairie Chicken (13)	C	18	21	0.56	4.5
Houbara Bustard (14)	C	87	6	0.56	7.0
Eagle Owl (15)	C	66	7	0.59	5.3
Florida Scrub-Jay (16)	C	24–248	31	0.59	6.0
Taita Thrush (17)	C	1–80	7	0.59	5.2
Eurasian Vulture (18)	C	10	5	0.65	5.0
Mexican Spotted Owl (19)	C	82–127	7	0.79	9.9
Corn Crane (20)	C	15	9	0.90	12.9

<sup>a</sup>Means are presented for genetic data, and ranges for the number of individuals sampled, when data were available from two or more subpopulations. Only data from wild populations or unrelated founders held in captivity are included.

<sup>b</sup>Reference codes: 1, Robertson et al. 2000; Miller et al. 2003; B. Robertson, unpublished data; 2, Tarr & Fleischer 1999; 3, Lieckfeldt et al. 2001; 4, Groombridge et al. 2000; 5, Mundy et al. 1997; 6, Grueber 2005; 7, Tepolt 2005; 8, Richardson et al. 2000; 9, Nesje et al. 2000; 10, Tarr et al. 1998; 11, Martinez-Cruz et al. 2002; 12, Hudson et al. 2000; 13, Bellinger et al. 2003; 14, Cbbel et al. 2002; 15, Isaksson & Tegelstrom 2002; 16, Stenzler & Fitzpatrick 2002; 17, Galbusera et al. 2000; 18, Mira et al. 2002; 19, Thode et al. 2002; 20, Gautschi et al. 2002.

<sup>c</sup>NZ, New Zealand species.

<sup>d</sup>Seven loci were all homozygous in 29 Kakapo from Stewart Island but were polymorphic in the one remaining Kakapo from Fiordland and in one museum specimen collected in 1884.

<sup>e</sup>Values were recalculated based on polymorphic loci only.

<sup>f</sup>Only observed heterozygosity is reported.

the Kakapo management team (Clout et al. 2002). Nevertheless, of the 67 eggs that were laid, 26 (39%) hatched, 25 (37%) were infertile, and a further 14 (21%) died at the embryo stage (Pain 2002). To put these figures in perspective, hatching success is > 90% in most birds (Koenig 1982). Most conservation geneticists would at least suspect that such poor hatching success could be due to inbreeding depression. In the case of the Kakapo, which has a history of poor productivity, high rates of hatching failure have been put down to an aging population and/or dietary problems (Clout & Merton 1998; Pain 2002). Only recently has greater effort gone into genotyping adults and their offspring to facilitate genetic management of the breeding population (B. Robertson & D. Merton, personal communication).

Placing too much emphasis on these two species can be misleading because every individual study has its flaws and can be criticized. On the other hand, these two case studies and Craig's (1991, 1994) arguments raise several broader questions: How common is genome purging in wild populations? To what degree are New Zealand's other land-bird populations ancestrally inbred? Do other inbred populations in New Zealand show signs of inbreeding depression? Will these inbred populations be viable in the future?

### Genome Purging in Wild Populations

Purging occurs when increased homozygosity resulting from inbreeding exposes recessive deleterious alleles to natural selection, thereby reducing the genetic load (Templeton & Read 1984; Hedrick 1994). In other words, successive generations of inbreeding may result in a rebound in fitness because of selective decrease in the frequency of deleterious alleles. Genetic drift can also result in purging, although it is a much less effective process than inbreeding stemming from nonrandom mating (Glémin 2003). The assumption that many of New Zealand's inbred bird populations have been purged of deleterious recessive alleles has not been verified empirically and is at odds with more recent views (Byers & Waller 1999; Keller & Waller 2002). Geneticists agree that genetic purging can eliminate lethal or semilethal alleles, but alleles of small effect will be much more difficult to purge because they are effectively invisible to selection (Charlesworth & Charlesworth 1987; Lande 1999). These small-effect detrimental mutations are likely to become fixed in small populations and thus cause a further increase in the genetic load (Hedrick 1994). Therefore continual inbreeding would not necessarily result in a rebound, but a further decline in fitness, and would push most small populations to extinction in the longer span of evolutionary time (Lynch et al. 1995; Lande 1999).

Most comparative and empirical studies of genetic purging support the conclusion that purging is unlikely

to reduce inbreeding depression (e.g., Ballou 1997; Byers & Waller 1999; Frankham et al. 2001). Nonetheless, Crnokrak and Barrett (2002) criticize many of these studies on a number of points, including a lack of controls. Their own review of controlled experimental studies found evidence for frequent and substantial purging for three different measures of fitness-component variation, and especially for reductions in inbreeding depression. Inbreeding in these experimental studies, however, mainly involved selfing in plants and sib-sib matings in mammals. Purging is much less effective when inbreeding results from random mating in small populations (Glémin 2003).

Based on modeling studies (e.g., Wang 2000), Keller and Waller (2002) concur that purging is unlikely to be common in natural populations because it requires rather restricted genetic and demographic conditions. They conclude that purging will not substantially reduce inbreeding depression for *most* field populations threatened by population reduction or habitat fragmentation (our emphasis). At least two of the four stated conditions, however—inbreeding occurs gradually and over several generations and the population is sufficiently isolated so that purged alleles are not reintroduced by immigration—could pertain to inbred island populations like those in New Zealand.

By contrast, results of a study of Collared Flycatchers (*Ficedula albicollis*) on the island of Gotland, Sweden (Kruuk et al. 2002), show one of the highest levels of inbreeding depression ever found in a wild population of birds. The authors suggest that this severity was consistent with a parent population with substantial genetic load and hence little purging as a consequence of its large size, low frequency of inbreeding, and high immigration rates. Based on this argument one might expect less (but not necessarily no) inbreeding depression in New Zealand endemics that have been isolated on small islands or habitat patches or have poor powers of dispersal and hence minimum gene flow and a long history of inbreeding.

### Degree of Ancestral Inbreeding in New Zealand's Bird Populations

Inbreeding and loss of genetic variation are inevitable consequences of small population sizes (Frankham et al. 2002). The extent to which a population becomes inbred or loses genetic diversity over time depends on a number of factors, including immigration, effective population size, generation length, and selection intensity.

It has often been assumed that many of New Zealand's extant land birds have gone through a long period of small population size and hence have a relatively long history of inbreeding (Craig 1991, 1994), although it is not clear on what this impression is based. Certainly there would have been reductions in population ranges during the last

glaciation about 10,000 years ago, but even at the height of the glaciation period most of New Zealand remained ice free and most likely would have supported relatively large populations for most species. Birds dominated the lowland forests of New Zealand, which were extensive and covered 80% of the landmass before Polynesians (about AD 800) and Europeans (1769) arrived (Atkinson & Millener 1991). Many of New Zealand's extant species went through major range contractions only soon after the 1800s, when extensive tracts of forest were cleared for farming and when rats, mustelids, and cats were introduced and became widespread (Clout 2001). Importantly, the populations that survived large-scale clearance of forests tended to be in more remote parts of the country or on islands, where there was little or no habitat modification and where introduced predators were slower to spread (Bell 1991). These isolated populations continued to decline due to predation until the mid-1960s and 1970s, when conservation efforts pertaining to predator control and island translocations intensified (Armstrong & McLean 1995; Clout 2001). These declines were large enough and long enough to have potentially resulted in inbreeding and loss of genetic variation, although perhaps no more so than what would have occurred on other oceanic islands where forest habitat was modified or mammalian predators were introduced. The declines may also have been gradual enough to allow, at least in theory, some genetic purging to have occurred.

Comparative analyses show that island populations in general, and threatened species in particular, have lower genetic variation than mainland populations (Frankham 1997; Frankham et al. 2002). Although one needs to exercise caution when comparing microsatellite data across species, threatened endemic birds on oceanic islands, including those in New Zealand, generally have lower genetic variation than threatened species from larger continental areas (Table 1). (Low levels of minisatellite variation, measured in terms of band-sharing coefficients, are also evident in three other threatened New Zealand endemics—Black Robin [0.84], Auckland Island Teal [*Anas aucklandica*] [0.71], and Shore Plover [*Thiornis novaseelandiae*] [0.56–0.68] [Miller et al. 2003].) Therefore the molecular evidence is at least consistent with the view that New Zealand's threatened endemic birds have gone through a relatively long period of small population size and subsequent inbreeding.

### Signs of Inbreeding Depression in New Zealand Populations

In contrast to earlier studies in New Zealand, in which the importance of inbreeding was generally downplayed, recent research has uncovered evidence of inbreeding depression in recent and in ancestrally inbred populations.

This work focuses on in-depth studies of endangered endemics and on broad comparisons among New Zealand birds.

The translocation of endangered species to isolated offshore islands has been one of the most successful conservation tools pioneered by New Zealand conservationists. However, some translocated populations of endangered species have much higher rates of egg infertility than populations of the same species that are also inbred but have remained in their native habitat (Jamieson & Ryan 2000). This is particularly true of the endemic Takahe (*Porphyrio hochstetteri*), a large (3 kg), flightless rail. Like Kakapo, Takahe occur in the subfossil record throughout New Zealand, but by mid-1870s, the only remaining population (approximately 250 birds) was isolated in the remote mountains of Fiordland. It is assumed that this single population continued to decline throughout the century (over an estimated 14 generations), reaching a low of approximately 100 birds by 1980, after which an intensive management program commenced (Lee & Jamieson 2001). Molecular evidence indicates that Takahe has relatively low genetic diversity in both translocated and source populations (Lettink et al. 2002; Grueber 2005; Table 1).

Takahe translocated from their native habitat in Fiordland to more temperate offshore islands have higher rates of survival but lay significantly more infertile eggs and raise fewer juveniles per egg (Jamieson & Ryan 2000). No specific environmental variables that can be directly linked to the poor fertility and hatchability of island Takahe eggs have been identified (e.g., Jamieson & Ryan 2001; Jamieson 2003). Jamieson and Ryan (2000) therefore propose that translocated Takahe and their descendants are suffering from environment-dependent inbreeding depression (e.g., Bijlsma et al. 1999) as evidenced by their much higher rate of reproductive failure than inbred Takahe living in their natural habitat in Fiordland. To test this hypothesis properly, inbred Takahe would also have to be translocated to islands with similar habitat type to that of the source population and their reproductive success compared. Although such comparisons have not been possible for Takahe, they have been carried out for translocated populations of South Island Tieke (or Saddlebacks) (*Ptiliastur c. carunculatus*) (Hooson & Jamieson 2004), and the results are consistent with the hypothesis of environment-dependent inbreeding depression. This hypothesis remains difficult to test because ideally one would like to compare reproductive success of a translocated outbred (or less inbred) population as well, but such populations do not exist for Takahe or Tieke.

The negative effects of more recent inbreeding in island Takahe, based on four generations of pedigree data, have also been documented. The inbreeding coefficient of the female (but not the male or the pair) had a significant affect on fledging success, reducing it by 81% (Jamieson et al. 2003). Jamieson et al. (2003) conclude

that the generally low fitness of Takahe introduced to islands could be a consequence of population-wide inbreeding depression through the fixation of deleterious alleles, whereas the effects of recent within-population inbreeding are more specific, with significant inbreeding depression occurring in inbred females but no detectable effects in inbred males or related pairs.

The lack of prebottleneck controls to study inbreeding depression is partly addressed by Briskie and Mackintosh (2004), who compared hatching failure rates in the multitude of bird species introduced to New Zealand (primarily from Europe) in the 1800s and 1900s. Unlike native species, introduced species still have large and outbred populations in their native range. Because the total number of individuals released per species ranged between 7 and 1500 individuals, Briskie and Mackintosh (2004) were able to compare hatching failure rates to the size of the bottleneck each species passed through during its establishment. Hatching failure increases with degree of inbreeding in other birds around the world and is one measure of the severity of inbreeding depression (Keller & Waller 2002). The greatest hatching failure among New Zealand populations of exotic birds was observed in seven species with < 150 individuals introduced. This was confirmed when they compared hatching failure before the bottleneck (i.e., in the source countries) and after the bottleneck (i.e., in New Zealand) with a matched-pair design. Differences in hatching failure rates between populations in their native and introduced ranges increased with the severity of bottleneck.

Briskie and Mackintosh (2004) also found the same relationship between hatching failure and population bottleneck in native bird species in New Zealand, with the highest mean failure rates observed in bottlenecks of <150 individuals (25.3%). Comparisons before and after bottlenecks were not possible for native species, but hatching failure in these populations was significantly higher than in those with bottlenecks of 300 to 5500 individuals (3.7%). Moreover, the level of hatching failure for bottlenecks of <150 birds was not significantly different between native (25.3%) and exotic (21.6%) species. This latter result is inconsistent with the hypothesis that native New Zealand species should be less susceptible to inbreeding depression than continental avifaunas.

None of the above evidence of inbreeding depression is quantitative in the sense of providing an estimate of the decrease in relative fitness per percentage increase in inbreeding. Such estimates would truly allow one to evaluate the degree to which New Zealand birds are more or less susceptible to inbreeding depression compared with species elsewhere. Nevertheless, recent qualitative evidence of inbreeding depression in bottlenecked populations of New Zealand birds still raises the question of whether inbred populations can recover despite exhibiting inbreeding depression and, if so, whether they will continue to be at increased risk of extinction.

## Viability of Inbred Island Populations

Cases have been documented from North America and Scandinavia of declining populations suffering inbreeding depression and then showing dramatic recovery after the introduction of new genetic stock (e.g., Westemeier et al. 1998; Madsen et al. 1999; Vilà et al. 2003). These cases are compelling, but because the populations had large and genetically variable sister populations, they do not closely parallel the situation of many island endemics. For example, the highly inbred Mauritius Kestrel (*Falco punctatus*) population has recovered from a single wild-breeding pair to more than 200 pairs without the addition of new genetic variation (Groombridge et al. 2000), as have several other threatened island species (Frankham et al. 2002). Similarly, as long as introduced predators are controlled or eradicated, inbred New Zealand endemics with low genetic variation generally show the capacity to increase dramatically without any introduction of new genetic stock (Armstrong & McLean 1995; Hooson & Jamieson 2004).

A recent attempt to model the release of small numbers of native passerines on predator-controlled islands in New Zealand has shown that these populations can exhibit a rapid increase in numbers, even when inbreeding depression in the form of egg failure is also severe (up to 66%) (Taylor et al. 2005). Initial high juvenile recruitment rates are particularly evident in reintroduced island populations because of density-dependent effects (Armstrong et al. 2005). Therefore any of the immediate negative effects of inbreeding on fitness traits such as egg fertility and hatchability can still be overcome through replacement clutches and multiple brooding producing rapid population growth, although the greater the inbreeding depression the longer it takes to reach the carrying capacity and the slower the recovery from any subsequent population catastrophes. Nonpasserine species that show signs of inbreeding depression but breed irregularly or have lower fecundity (e.g., Kakapo and Takahe) may require more intensive genetic management to facilitate population recovery.

Although the short-term negative consequences of inbreeding may not necessarily prevent recovery of some species, the long-term consequences of inbreeding are potentially much more insidious. This is because inbreeding in small populations almost invariably leads to loss of genetic variation, and such populations are less responsive to selection pressures. One particular concern is that reduced variation in loci associated with the immune response could make inbred individuals more susceptible to introduced diseases and pathogens (e.g., Reid et al. 2003). Although this may turn out to be generally true, threatened New Zealand bird populations are increasingly being managed to minimize the introduction of avian diseases whether the populations are inbred or not. How then could a link between inbreeding and disease

susceptibility affect management guidelines in New Zealand? One possibility is that greater effort could go into maximizing founder representation at the initial translocation stage or employ interpopulation crosses to maximize genetic variation (e.g., Haig et al. 1990; Westemeier et al. 1998; Ralls & Ballou 2004). Even if outbred populations do not exist, which is commonly the case in New Zealand, crosses between two or more independent inbred populations with loci fixed for different alleles can be used to increase heterozygosity, allowing recovery of fitness (Frankham et al. 2002). Such measures have yet to be adequately tested with New Zealand birds but may be useful for managing populations currently showing high levels of inbreeding depression such as increased egg failure.

## Conclusions

There is increasing evidence that many threatened populations of New Zealand birds suffer a loss of fitness as a consequence of bottlenecks and inbreeding. It is still not clear, however, whether the pattern of inbreeding depression is different from that of threatened species found elsewhere, especially those with reduced distributions relative to their former continental ranges. Nevertheless, the overwhelming evidence from dozens of studies (both theoretical and empirical) suggests that limiting the potential negative effects of inbreeding and loss of genetic variation should be an integral part of any management program of the many small, isolated, and highly inbred native bird populations found in New Zealand. Failure to do so could result in reduced fitness potential and greater susceptibility to biotic and abiotic perturbations in the short term and reduced ability to adapt to environmental change in the long term. The degree to which genetic factors reduce population viability generally remains unquantified in New Zealand. In the meantime, minimizing ecological risks (e.g., preventing reinvasion of islands by mammalian predators) will continue to take precedence because of their much larger, short-term impacts. One of the challenges for New Zealand conservation biologists is to quantify the long-term risks implicated in broad-scale genetic models so that they can be included in fine-scale viability models adapted to local (New Zealand) conditions.

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