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RESEARCH ARTICLE

Quantifying and managing the loss of genetic variation in a free-ranging population of takahe through the use of pedigrees

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Abstract Pedigree analysis has clear benefits for the genetic management of threatened populations through the evaluation of inbreeding, population structure and genetic diversity. The use of pedigrees is usually restricted to captive populations and few examples exist of their exclusive use in managing free-ranging populations. One such example is the management of the takahe (*Porphyrio hochstetteri*), a highly endangered, flightless New Zealand rail at risk from introduced mammalian predators and habitat loss. During the 1980's and 90's, as part of the takahe recovery programme, birds were translocated from the sole remnant population in Fiordland to four offshore islands from which introduced predators had been eradicated. The subsequent "island" population, now numbering 83 and thought to be at carrying capacity, has been closely monitored since founding. Detailed breeding records allow us to analyse the island pedigree, which is up to 7 generations deep. Gene-drop analysis indicated that 7.5% of genetic diversity has been lost over the relatively short timeframe since founding (2.1 generations on average; total genetic founders = 31) due to both a failure to equalise founder representation early on and subsequent disproportionate breeding success (founder equivalents = 12.5; founder genome equivalents = 6.6). A high prevalence of close inbreeding will have also impacted on genetic diversity. Predictions from pedigree modelling suggest that 90% genetic diversity will be maintained for only 12 years, but by introducing a low level of immigration from the Fiordland population and permitting the population to grow, 90% GD could be maintained over the next 100 years. More generally, the results demonstrate the value of maintaining pedigrees for wild populations, especially in the years immediately after a translocation event.

Keywords Founders · Genetic diversity · Heterozygosity · *Porphyrio hochstetteri* · Threatened species

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Introduction

Avoiding inbreeding and maintaining genetic diversity are primary goals for managing captive populations of endangered species. Pedigrees have proven to be an invaluable tool in managing captive populations, in particular for providing a direct means of evaluating inbreeding coefficients, for identifying genetically rare individuals or founder lineages, as well as for monitoring changes in overall levels of genetic variation (Frankham et al. 2002; Earnhardt et al. 2004; Ralls and Ballou 2004).

Pedigrees can also be useful in the management of wild populations by providing detailed views of population structure, genetic diversity and potential viability that would otherwise be difficult to obtain (Haig and Ballou 2002). Molecular tools are being used increasingly to estimate genetic diversity and infer levels of inbreeding and relatedness in unpedigreed wild populations, but their utility can be limited when the proportion of polymorphic loci is small, as is often the case for many threatened populations (Jones et al. 2002; Jamieson et al. 2006). Indeed, pedigrees are likely to provide a more reliable estimate of levels of inbreeding and relatedness than genetic markers (Pemberton 2004). In addition, the use of molecular markers may not be the most effective method

for understanding the relative importance of specific individuals in managed populations, whereas pedigrees allow a much more direct approach of assessing the level of inbreeding or loss of genetic diversity over time for a defined group of individuals (Haig and Ballou 2002). However, pedigrees are difficult to reconstruct and maintain in wild populations, and there are few examples of their use in conservation management (Haig and Ballou 2002). Furthermore, even if pedigree data were available, it is not clear how they could be used to manage breeding pairs in a free-ranging population where individuals are able to choose their own mates.

Here we use pedigree analysis to calculate such measures as effective number of founders and founder genome equivalents (Lacy 1989), and to evaluate the loss of genetic diversity and identify the reasons for the loss in a free-ranging population of the highly endangered takahe *Porphyrio hochstetteri*, a flightless rail that has been introduced to several of New Zealand's offshore islands. We also show how 'gene-drop' analysis (MacCluer et al. 1986) and the so-called 'one-migrant-per-generation' rule (Mills and Allendorf 1996) can be applied to the long-term management of an inbred but free-ranging population. More generally, this study, along with a small number of others (Haig and Ballou 2002; Ralls and Ballou 2004), illustrates the benefits of collecting pedigree information from the beginning of a reintroduction programme.

Species background

Takahe are endemic of New Zealand, are the world's largest ($\sim$3 kg) flightless rail species and one of the rarest (Taylor and van Perlo 1998). By the end of the 1800s, takahe were thought to be extinct until the discovery in 1948 of a remnant alpine population in remote Fiordland in the South Island (Lee and Jamieson 2001). Takahe are primarily under threat from introduced predators, such as rats and mustelids, as well as introduced deer which browse heavily on the takahe's main food source of native tussock grasses. Therefore, in the 1980s, the New Zealand Department of Conservation established an additional population outside the current range, on 4 offshore islands from which introduced predators and browsers had been eradicated (for location maps and details of translocations, see Jamieson et al. 2003). A total of 25 Fiordland birds (mostly juveniles), which were the offspring of banded territorial pairs, were introduced gradually to these islands between 1984 and 1999 (Fig. 1). The island population now totals 83 birds. Because each island and its available habitat is relatively small (see below), takahe have been managed as a single population: occasional transfers are permitted between islands but not back into Fiordland because of the risk of introducing disease (D. Crouchley, Department of Conservation, pers. comm.).

Takahe are free to form 'natural' pairings on the islands, and breeding is closely monitored; every offspring is colour-banded on its natal territory, given a name and entered into the studbook. Molecular evidence indicates that breeding pairs are genetically monogamous (Lettink et al. 2002). The resulting complete pedigree, based on 18 years of data, is one of the longest for a non-captive endangered species. Many of the current juveniles are fourth generation island-raised birds, although pedigree information for some individuals extends back as far as seven generations. Patterns of inbreeding and inbreeding depression derived from the pedigree information have been published previously (Jamieson et al. 2003).

Methods

Pedigrees for takahe on each of Tiritiri Matangi (220 ha), Maud (309 ha), Mana (217 ha) and Kapiti (2,023 ha) Islands were constructed using field data collected by the Department of Conservation and maintained in SPARKS v1.42 (ISIS 1992). Takahe start breeding at 2 years of age (modal clutch size of 2 eggs) and can live up to 20 years, hence generations overlap in the pedigree. Birds that were alive in October 2004, and all their known ancestors, were included in the pedigrees; birds that died without producing any descendents are excluded from the gene-drop analysis (see below). The word "founder" is used here to imply a "genetic founder" and not simply birds that were released onto the islands. Furthermore, it is not required that genetic founders were ever part of the island population, only that they have at least one living descendant so that a portion of their genome is represented in the current island population. These founders are banded birds from Fiordland between which relatedness is unknown, but which are the parents of the translocated birds and hence located at the top of the pedigree.

Extra-pair fertilizations and female "egg-dumping" are rare or absent in takahe, and so the resident territorial birds are almost certainly the parents of any offspring (Lettink et al. 2002). A few takahe breed in groups of two adult males and/or two adult females which are unrelated (i.e., non-sibling groups) and thus exact parentage of 10 of 136 birds in the pedigree (excluding the founders) could not be determined by observation alone. A previous study using minisatellite DNA, did not detect enough genetic variation for parentage to be assigned definitively, however in all cases the resident adults were not excluded (Lettink et al. 2002). Parentage has now been assigned for two of these birds using microsatellite DNA (Grueber 2005). In those cases where parentage could not be assigned, again the

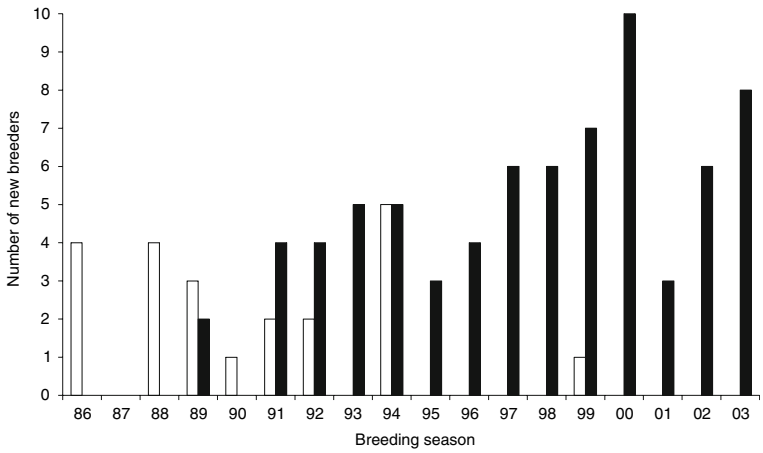

Fig. 1 The source of new island breeders in each breeding season, between 1986 and 2003, subdivided into those takahe that were originally translocated (open bars) and those that were island-raised (offspring of translocated birds—black bars), over all 4 island sites

putative resident parents could not be excluded. Therefore, in 8 cases where the actual father or mother is unknown, parentage was assigned randomly from the same-sex breeders within the resident group, and the resultant pedigrees were used in the analysis. Alternative analyses using different parentage assumptions (assigning parental combinations that resulted in either maximal or minimal inbreeding coefficients), did not change the overall conclusions (Grueber 2005). Random assignment was retained as it is the most biologically likely scenario based on parentage studies of a closely related species, the pukeko (*Porphyrio porphyrio*) which regularly breeds in same-sex groups of unrelated adults (Jamieson et al. 1994; Jamieson 1997).

Individual inbreeding coefficients (F) were calculated using SPARKS (ISIS 1992), and corroborated using PM2000 (Pollak et al. 2002). Using PM2000, we also generated three pedigree-based statistics: the number of founders, founder equivalents and founder genome equivalents, which can be compared to evaluate structure within the pedigree. The number of founders is simply the number of individuals at the top of the pedigree, for which no pedigree information is available and so are presumed unrelated. Founder equivalents, denoted f_e, represents the expected number of equally-contributing unrelated founders that would give rise to the observed level of genetic diversity in the study population, thus providing a relative measure of the variance in founder representation. An f_e value that is close to the number of actual founders suggests proportional representation from each founder in the descendant population. Founder genome equivalents, denoted f_g, represents the expected number of unrelated founder genomes that would contain the observed level of genetic diversity in the study population and is generally estimated by gene-drop simulation (Lacy 1989; Haig and Ballou 2002; Pollak et al. 2002). As f_g increases towards f_e, the proportion of founder alleles that are retained in the descendant population also increases, thus reducing the amount of genetic diversity that has been lost since founding (Lacy 1989). Values of f_e or f_g that are much lower than the total number of founders normally indicate a small number of founders producing disproportionately large numbers of offspring. In addition, an f_g value that is much lower than f_e for a given population suggests that some alleles have been lost due to genetic "bottlenecks" or other structuring within some founder lineages, for example, if only one or a few offspring were produced shortly after founding, despite subsequent descendents in that lineage breeding well (for further details see MacCluer et al. 1986; Lacy 1989; Haig et al. 1994).

PM2000 also calculated mean kinship (MK, equal to the loss of gene diversity in the descendant population relative to the founders) and gene diversity (GD, the proportion of heterozygotes expected in the descendant population under Hardy–Weinberg assumptions relative to the founding population). Retained GD is calculated by assigning two unique hypothetical alleles to each founder and running a gene-drop simulation analysis to evaluate what proportion of the starting GD remains in the current population. In a gene-drop analysis, the hypothetical alleles assigned to the founders are "dropped" down through the known pedigree (which is entered by the user) from one individual to the next according to Mendelian inheritance. The alleles that remain at the bottom of the pedigree (in the living population) are counted, and 10,000 iterations provide probabilities of allele and GD retention by simulating the stochastic nature of inheritance across an individual's genome (MacCluer et al. 1986; Lacy 1989; Haig et al. 1990; Pollak et al. 2002; Ralls and Ballou 2004). Founder genome equivalents (f_g) are calculated similarly by gene-drop analysis. Only living, non-founding birds in the current population are used in the calculation of these statistics (Lacy 1989), and the gene-drop analysis only

evaluates contribution of the genetic founders to the current population.

Using the current population size (83), calculated remaining GD, and estimated growth rate (1.081, calculated from input data) and generation time (7.2 y, calculated from input data) it is possible to use PM2000 to evaluate management strategies for maintaining genetic diversity and the beneficial effects of introducing new founders over a given time frame, in this case 100 years. Shorter time periods have been advocated (for example, Earnhardt et al. 2004 used only 10 years for projections; while Kuo and Janzen 2004 used 200 years), but 100 years is standard practice in many population genetic models (Allendorf and Ryman 2002; Frankham et al. 2002). The longer time frame seems particularly appropriate in this case because takahe are a relatively long lived species (see above). It is thought that the island population has reached carrying capacity, as indicated by the large number of non-breeding adults on each island (Grueber and Jamieson, unpubl. data). Strategies were evaluated under two population size assumptions: (1) the current total island population (83 birds including juveniles) at carrying capacity (a conservative estimate resulting in the highest rate of genetic diversity loss by drift); and (2) allowing the total population to increase by 19 birds to 102 individuals (19 represents the average population size of the 4 other island sites), to simulate the establishment of a fifth island site. The migration analysis assumed that each additional founder brought in contributes an average 0.400 f_g to the population (calculated by PM2000 from the input data).

Results

We first focus on the birds that were introduced to the islands and their variable contribution to the number of living descendants. About 8 of the 25 (32%) introduced birds from Fiordland either did not breed on the islands or left no descendants in the current population. Of those birds that did breed, some were much more successful than others resulting in a large proportion of living descendents with lineages that can be traced back to a group of only a few birds/pairs. For example, 43 and 42 of the 83 birds in the current population (52–51%) can trace their lineage back to a particular translocated pair named Squeak (female) and Taku (male), respectively. Overall, there was a significant correlation between the number of adult years resident on the islands and the number of descendants (males and females analysed separately: $r_{males} = 0.518$, $p = 0.048$, $N = 15$; $r_{females} = 0.639$, $p = 0.047$, $N = 10$).

We then carried out a formal analysis of the genetic founder contribution, which involved all birds in the pedigree, including known ancestors that were a part of the source population in Fiordland. The total number of genetic founders for the current island population of takahe is 31 (all of which are Fiordland birds), although the proportion of descendents each has contributed is highly skewed (Fig. 2). Due to this skewed distribution, the number of founder equivalents ($f_e = 12.5$) and the number of founder genome equivalents ($f_g = 6.6$) are low relative to the number of genetic founders. The value for f_g is much lower than f_e, indicating that many of the genetic founders contributed only one or two offspring, despite the fact that these offspring then went on to breed successfully.

Although many of the current juveniles in the island population are 4th–6th generation, the average generation time of takahe is relatively long for a bird (estimated to be 7 years), which means that most of the island birds contributing to the analysis have gone through an average of only 2.1 generations since establishment (based on a median date of release of 1989 and 15 years of breeding). Nevertheless, gene diversity (GD) is currently 0.925,

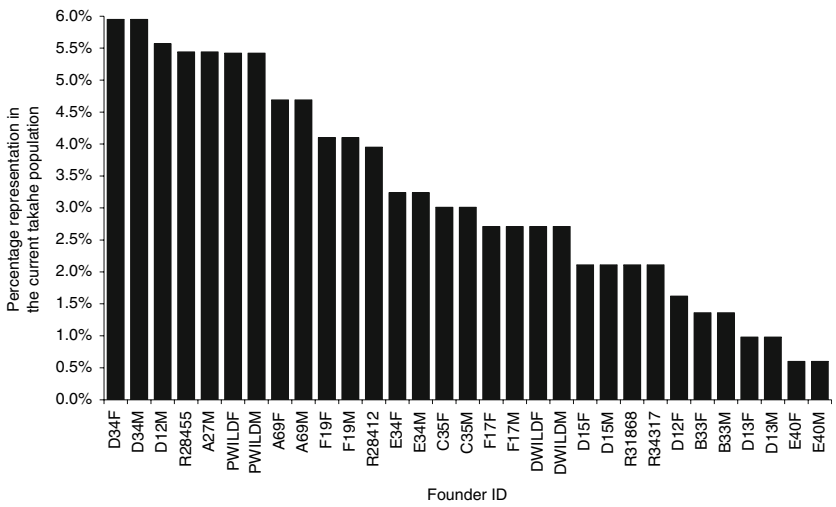

Fig. 2 Percentage of the current island takahe population that is represented by each of the 31 genetic founders to the population. Founder ID refers to a known Fiordland individual. Under the null hypothesis that *f*e = founder number, each bar would be equal height; note that in this population *f*e = 12.5

indicating that the island takahe population has already lost 7.5% of the original heterozygosity in the founding population. In addition to disproportionate founder representation, inbreeding would have also contributed to a loss of heterozygosity. Inbreeding was common in the takahe pedigree: 36 of 83 (43%) living birds were inbred, 23 of these (64%) with $F \geq 0.125$ (close-inbreeding). The overall mean level of inbreeding among the current breeding population is 0.089 (SE = 0.016), one of the highest levels for a bird population in the wild (see Table 3 in Jamieson et al. 2007).

We then asked which management options could slow further losses of genetic variation. A standard recommendation provided by many management programmes is that they should attempt to maintain at least 90% of the genetic diversity found in the wild or source population (Lacy 1989). Our computer simulations predicted that without any management intervention, 90% GD (of the original genetic founders) in the island takahe population would be maintained for only 12 years, and would decline to 76% after 100 years if the population remains at carrying capacity (Fig. 3A). Allowing the population to increase by establishing a new island site with a carrying capacity of 19 birds (see "Methods") could maintain 90% GD for 15 years and would decline to 79% GD after 100 years (Fig. 3B). Under the one-migrant-per-generation rule of thumb (Spieth 1974; Mills and Allendorf 1996; Wang 2004), the 90% GD retention times are increased to 17 and 24 years, respectively (Figs. 3C and 3D). Based on these estimates, if the retention of 90% GD over 100 years is set as the overall management goal for the island takahe, then 2 new founders every 4 years would be required at the current population size, or every 5 years if a new island site is established. The founding of additional island sites would further reduce the required period between immigration events.

Discussion

The primary aim of this study was to demonstrate how pedigrees and pedigree analyses can be integrated into management plans for maintaining genetic variation in a free-ranging population of an endangered species. Our analysis indicated that significant losses of genetic variation in endangered takahe could have been prevented if greater effort had gone in to equalising founder representation during the establishment phase of the island translocation programme. Like many recovery programmes in New Zealand (Jamieson et al. 2006), takahe translocated to island refuges were managed to maximize productivity and population growth rate, partially at the expense of retaining genetic diversity. A failure to equalise founder representation in growing populations can lead to a reduction in genetic diversity and increased inbreeding (Haig et al. 1990; Meffert et al. 2005).

To limit further loss of genetic diversity, we recommended that one or more new island sites be established as well as introducing 2 new breeding birds into the breeding population every 4–5 years. Unlike a captive breeding situation, it is not practical to select unrelated pairs to promote outbreeding; in the case of takahe, penning unrelated birds as a means of force-pairing has had limited success (Takahe Recovery Group, unpubl. data). Translocation between islands provides the most effective means of reducing the incidence of close inbreeding.

Other approaches for managing and maintaining genetic diversity of a population include equalising sex ratios and family sizes and avoiding fluctuations in population size (Caballero and Toro 2000). As shown in this analysis and by others (Lacy 1987; Mills and Allendorf 1996; Bijlsma et al. 2000) increasing population size and allowing a low rate of immigration may be the most effective means of reducing the rate of further genetic diversity loss in small,

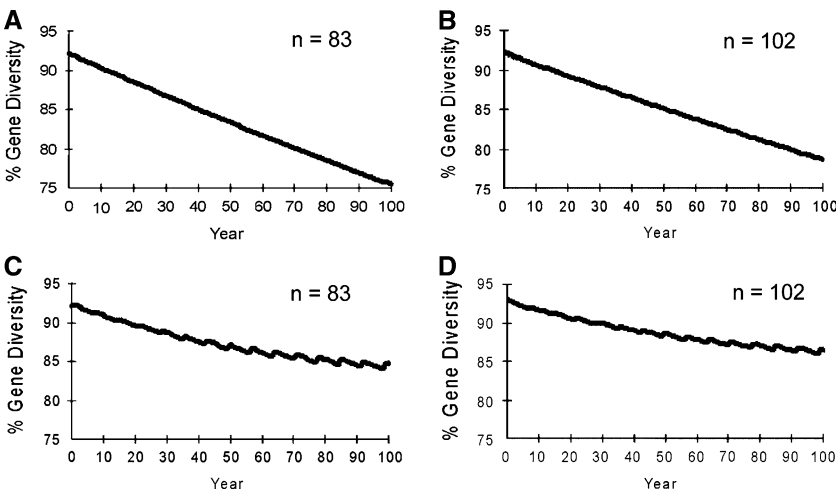

Fig. 3 The predicted loss of genetic diversity over time for two different maximum population sizes (N = 83 and 102) with either no immigration (A–B) or 1 immigrant per generation (C–D) as reflected by the small increases in GD at the time of each immigration event. (Note the scale of the y-axes ranges between 75 and 95% GD)

closed populations. Although there may be logistical and financial factors that would need to be considered before implementing either of these strategies, without any intervention, the island takahe population is projected to maintain only 76% of the original founding genetic diversity in the next 100 years.

Finally, our study raises two fundamental questions: how much genetic diversity is enough, and does the genetic diversity that is being quantified have functional consequences? First, maintaining 97.5% of the founding genetic diversity has been considered ideal for captive populations (Lacy 1989), although a "more, the better" attitude is widely adopted (Franklin and Frankham 1998; Lynch and Lande 1998; Gautschi et al. 2003). The most widely cited standard for long-term management programmes is to set a target of 90% (Lacy 1989; Frankham et al. 2002) or 95% (Allendorf and Ryman 2002) of the heterozygosity in a population over 100 years. In a threatened wild population that has already undergone a genetic bottleneck, the aim is often set at 80–90% retained GD, depending on the size of the population, GD already lost and the resources available for genetic management of the population. Although we know of no recovery programme in New Zealand that sets specific targets, other international avian recovery programmes aim to maintain 80–90% of GD (Guam rail, Haig and Ballou 1995; whooping crane, Jones et al. 2002; bearded vulture, Gautschi et al. 2003; ʻAlala [Hawaiian crow], US Fish and Wildlife Service 2003; Californian condor, Ralls and Ballou 2004). As just over 92% of the original GD is currently present in the island takahe population, aiming to maintain 80–90% of GD over 100 years could be a reasonable goal for a long-lived bird.

Second, the underlying assumption of gene-drop simulations and pedigree analyses in general is that the predicted loss of genetic diversity over time is affecting functional genes and not just neutral genetic variation. This assumption is increasingly being questioned, prompting studies of the effects of population bottlenecks on parts of the genome such as MHC (Major Histocompatibility Complex) loci, which play a role in the immune system and are thought to be maintained by balancing selection (Hughes and Yeager 1998; Hughes 2002). Nevertheless, a comprehensive study of the endangered black robin (*Petroica traversi*) (Miller and Lambert 2004) indicated that soon after a bottleneck, variation at MHC loci is lost by drift comparably to neutral variation, despite the fact that variation at MHC loci over the long term is likely to be maintained by balancing selection. Similarly, a recent study comparing neutral (microsatellite) and functional (MHC) markers in nine isolated trout (*Salmo trutta*) populations demonstrated that, when populations are small, drift may have a more significant effect on genetic diversity than selection, at least in the short term (Campos et al. 2006). The results of these two studies suggest that, at least for small or recently bottlenecked populations, genetic modelling based on neutral markers may provide a useful barometer for genetic diversity at certain functional loci, such as MHC.

In conclusion, this study provides a rare example of how pedigree data can be successfully integrated into the genetic management regime for an endangered species that is free-ranging.

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