

## SHORT COMMUNICATION

### Are introduced takahe populations on offshore islands at carrying capacity? Implications for genetic management

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**Abstract:** Translocation to island reserves is a common strategy in New Zealand and elsewhere for safeguarding species against introduced predators. When successful, however, the closed nature and relatively small size of many island sanctuaries can result in populations quickly reaching their carrying capacity, which in itself can present further challenges such as reduced productivity and population growth rates associated with density-dependent effects as well as increased rates of inbreeding. As part of its management strategy, small numbers of the highly endangered takahe (*Porphyrio hochstetteri*) were translocated during the 1980s and 90s from the last remaining natural population on the mainland of New Zealand to four offshore islands where introduced predators had been eradicated. We used logistic regression and generalised linear models to assess trends in population growth and recruitment and to evaluate whether the island metapopulation displays density-dependent effects on productivity. Our results indicate that the island metapopulation appears to have reached its carrying capacity, as reflected in an increasing ratio of non-breeding to breeding adults, and recent declines in juvenile production. These density-dependent effects are likely to constrain management strategies aimed at maintaining genetic diversity and minimising inbreeding. A recommendation to increase the immigration rate of takahe onto islands via translocations of birds from the source population on the mainland may be ineffective unless surplus birds are removed.

**Keywords:** density dependence; New Zealand; recruitment; threatened species; translocation

## Introduction

Translocating threatened endemics to island reserves or fenced mainland sanctuaries is a common management strategy in New Zealand and elsewhere for safeguarding species against introduced predators (Clout 2001; Bellingham et al. 2010). Such approaches have been generally successful in New Zealand and island populations now contribute significantly to the total population of many threatened species (Saunders & Norton 2001; Innes et al. 2010). However, the genetic consequences of establishing island populations with small numbers of founders and a limited carrying capacity have been largely overlooked (Jamieson et al. 2006; Jamieson 2011), even though small populations are subject to losses of genetic diversity due to founder effects and genetic drift, as well as high levels of inbreeding, all of which can erode evolutionary potential and long-term viability (Frankham et al. 2002; Jamieson et al. 2008).

The rate at which populations lose genetic diversity and become more inbred is primarily determined by population growth rates and final population size, both of which are influenced by carrying capacity of the habitat (Jamieson 2011). As a population approaches its carrying capacity, density-dependent effects on productivity, recruitment and/or survival should, in theory, slow population growth rates. Although density-dependent effects on growth rates are notoriously difficult to detect statistically (Wolda & Dennis 1993; Fox & Ridsdill-Smith 1996), assessing density-dependent influences on vital rates (reproduction and survival) is less problematic

(Elkinton 2000). Island introductions are ideal for studying these processes because individuals are usually introduced at a low density, thus providing the opportunity to examine how vital rates change as populations grow (Nicoll et al. 2003; Armstrong et al. 2005). Armstrong et al. (2005) have argued that density dependence is a critical issue for our understanding and management of island reintroductions, especially in assessing population viability and consequences of harvesting individuals for further reintroductions. Here we examine possible effects of density dependence on productivity and recruitment in introduced island populations of takahē (*Porphyrio hochstetteri*), and how these processes might ultimately affect genetic management.

In order to reduce the risk of extinction, 25 takahē (mostly juveniles) were translocated between 1984 and 1999 from the last remaining natural population in the Murchison Mountains in Fiordland to offshore islands of Kapiti, Mana, Maud and Tiritiri Matangi, from which introduced predators and pests had been removed (for maps and details of translocations see Lee & Jamieson 2001; Grueber & Jamieson 2008; see also Methods). The island birds have been managed as a closed metapopulation, with occasional translocations among islands (Jamieson & Wilson 2003). Nevertheless, the island takahē population displays a high level of inbreeding (Jamieson et al. 2003; Grueber & Jamieson 2008; Grueber et al. 2010; Jamieson 2011), which has been shown to impact long-term individual fitness (Grueber et al. 2010), and therefore potentially to harm population viability. Given recent recommendations to regularly introduce new founders to the island population

(Grueber & Jamieson 2008), it is important to determine whether these new birds are likely to establish breeding territories. The predicted high density of breeding pairs across the islands (Ryan & Jamieson 1998) has not been realised, and the presence of large numbers of single adult takahē on each of the islands and more frequent signs of aggression (D. Eason, unpubl. report) suggests that the population may be close to or at carrying capacity. If so, then introductions from Fiordland will be ineffective at decreasing island population mean kinship if the new birds are unable to breed and thus contribute to the gene pool.

The goal of this study was to examine trends in population growth and recruitment rates of the island population of takahē to determine whether the carrying capacity (measured in terms of number of breeding pairs/groups) for each of the islands has been reached. We test whether the island takahē population has maximised the number of breeding pairs as well as evaluate possible density-dependent effects on productivity and recruitment. We then discuss how the results could impact on strategies to manage genetic diversity through translocation and immigration.

## Materials and methods

We used breeding records and data on population size maintained by the Department of Conservation (DOC) to evaluate population growth and recruitment over 24 years from 1986, when breeding first occurred on the islands, up to and including the 2009/10 breeding season. The total available takahē habitat across all four islands has been estimated at approximately 248 ha – 43 ha on Kapiti, 62 ha on Mana, 57 ha on Maud (Ryan & Jamieson 1998) and 86 ha on Tiritiri Matangi (Baber & Craig 2003) – but takahē on the four islands are managed collectively, with regular translocations amongst them, and are considered as a single population (Wickes et al. 2009). In this analysis we therefore evaluated data from the population as a whole, while including island as a fixed factor in our models to account for habitat differences on the islands.

We first examined whether the islands are supporting a maximum number of takahē both in terms of adult population size and number of breeding pairs/groups (as an indication of whether all potential breeding sites are being used). These data were used to calculate whether the proportion of non-breeding adults across the islands has changed over time. To do this, we used logistic regression where number of adults was the binomial denominator and number of breeders was the binomial numerator (event); year and year<sup>2</sup> were fitted to account for curvature in the model.

We next examined whether density-dependent effects were impacting the production of juveniles in the island population. To do this, we examined number of juveniles produced per adult as a function of total number of adults across the islands. We fitted a generalised linear model with a quasi-Poisson link function to account for overdispersion in the response variable. As both the longevity and territoriality of takahē have resulted in a gradual increase in the age of breeders on the islands since founding (mean age ~ year: standardised  $\beta = 1.40$ , adjusted SE = 0.252, 95% CI for  $\beta = 0.901, 1.89$ ), we calculated the annual mean age of breeders (across the entire population) to control for any possible effects of senescence. A small number of breeders (9 of 146) with uncertain age (i.e. immigrants) were excluded from calculation of the predictor variable for annual mean age, but were otherwise retained in the analyses.

To assess whether density-dependent effects of the carrying capacity of the islands are evident, we evaluated whether recruitment rates onto territorial sites declined as population size increased. Our recruitment models used population size rather than year as a predictor to control for any effects of translocations into (9 subadults and 23 adults) and out of (15 subadults and 9 adults, from 2005 onwards) the island population. Nevertheless, year and population size were highly correlated ( $r = 0.963$ ). Our recruitment response variable followed a binomial distribution, where the number of birds that were competing to breed for the first time on an island (either due to reaching breeding age, 2 years, or following a translocation as an adult) was the binomial denominator, and the number successful in establishing a territory was the binomial numerator (event). A logistic regression was fitted in R (R Core Development Team 2011) with island site, adult population size and the interaction of these two factors, as predictors.

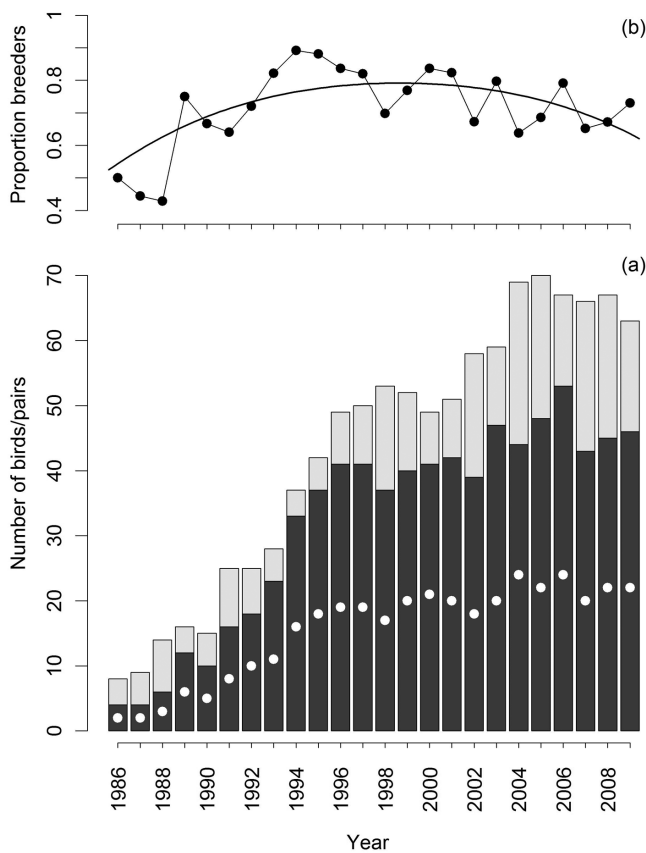
For birds that did successfully recruit, we further examined whether time to recruitment was dependent on population size. Time to recruitment was quantified as number of *adult* years until first breeding. For example, an island-hatched bird that bred in its first adult year (at 2 years of age) was scored as a '1', in its second year as a '2', and so on. Taking this approach (rather than using raw age-data) allowed us to compare recruitment times of both local birds and immigrants in the same model, where immigrants were similarly scored for their first, second, etc. adult year in the population, regardless of age at translocation. Translocations among islands were accounted for, but only those that occurred prior to first breeding. This latter analysis was performed at the level of all four islands collectively, due to low numbers of immigrant birds per island.

All models were fitted using R (R Core Development Team 2011). We used functions available in the R package 'arm' (Gelman et al. 2009) to standardise (and back-transform) model predictors following Gelman (2008), as this improves interpretability of parameter estimates, particularly where polynomials and interactions were fitted, and continuous and categorical factors are combined in the same model. For each analysis we first fitted a global model, containing all predictors as described above, and then used functions available in the R package 'MuMIn' (Bartoń 2009) to generate a model set of all possible sub-models, ranked by AIC<sub>C</sub> (corrected Akaike Information Criterion). If the best model had an Akaike weight < 0.9 (Burnham & Anderson 2002) we used model-averaging to generate final parameter estimates from which inference was based, as this approach allows us to incorporate model selection uncertainty into our parameter estimates and their standard errors. Model-averaging parameter estimates from a GLM with a quasi-Poisson link (i.e., rate of juvenile production) can produce inaccurate error estimates if data were overdispersed, but overdispersion in our dataset was very low (dispersion parameter = 0.0896) and parameter estimates based on the global model were in the same direction and of similar magnitude to those produced by model-averaging. As we had no a priori expectations regarding relative magnitudes of year, island, or population-size effects, we averaged the 95% confidence-level set of models using the zero (shrinkage) method (following Grueber et al. 2011). We report the model-averaged standardised regression coefficients as an indication of effect sizes, along with 95% confidence intervals as a measure of their precision (Nakagawa & Cuthill 2007; Gelman 2008). We also report the relative importance of each predictor, which is the summed posterior Akaike weights of

the models containing that parameter that were included in the averaged model set. Relative importance thus provides a further measure of the degree of support for each parameter that was retained in the final model set, and has a maximum value of 1.0 (Burnham & Anderson 2002).

### Results

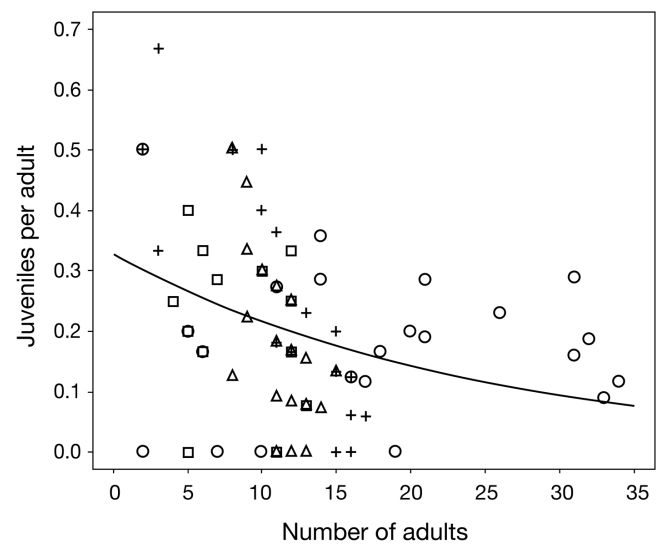
Since breeding first occurred on the islands in 1986, the population has increased to 63 adult takahē in the 2009/10 season, of which 46 birds were breeding in 22 pairs/groups (Fig. 1a). The observed maximum adult population size in a breeding season over the history of the islands was 70 takahē (in 2005), and the maximum number of breeding pairs/groups was 24 (in 2004 and 2006). Despite increasing population size, the proportion of breeding adults has decreased in more recent years (Fig. 1b, logistic regression final model [standardised  $\beta \pm$  adjusted standard error]: proportion of adults breeding  $\sim 0.318 \times \text{year}[\pm 0.302] - 1.5 \times \text{year}^2[\pm 0.515] + 1.300[\pm 0.114]$ ; note the large negative effect of  $\text{year}^2$  relative to its standard error). Even with the decline in the proportion of adults that are breeding, there has still been a slight increase in the mean breeding-group size on the islands since founding (breeders per pair  $\sim \text{year}$ : standardised  $\beta = 0.070$ , adjusted SE = 0.061, 95% CI for  $\beta = -0.050, 0.19$ ).



**Figure 1.** Annual takahē population trend across all four islands since breeding first began in 1986. In (a), the bars indicate the total number of adults, of which the dark portion indicates the number breeding; the open circles indicate the number of breeding pairs/groups in each year. (b) illustrates the proportion of adult takahē that were breeding in each year; the fitted trend line is a logistic regression with year and  $\text{year}^2$  fitted as fixed factors (see Results).

The annual number of juveniles produced per adult (juvenile production) was highly variable across all levels of population density (Fig. 2). However, the general trend was a decrease in juvenile production as population sizes (i.e. number of adults) increased, even after accounting for differences between islands and the increasing mean age of breeders (the confidence interval of the effect size for number of adults excludes zero; Table 1). The relative importance of number of adults in the model was 1.0, indicating that all models in the top model set contained the number of adults as a predictor. By comparison, the relative importance values of island site and mean age of breeders were lower, indicating that only a proportion of models in the top set contained these predictors (Table 1).

In contrast to juvenile production, there was only weak evidence for an effect of population size on subsequent annual recruitment rates. Although the model-averaged output indicated that there was a negative relationship between number of adults and proportion of individuals that successfully recruited, the effect had very poor precision (confidence interval for the effect size was wide and included zero; Table 2). Recruitment rates differed across sites with Mana and Tiritiri Matangi islands both having higher recruitment rates than Kapiti Island (Table 2). There was only limited support for different demographic effects across islands on recruitment, as the relative importance of this interaction after model averaging was 0.20, and in all cases the confidence intervals for the effect size were wide and included zero (Table 2). Population size was not a useful predictor of the number of adult years to first breeding (generalised linear model final model [standardised  $\beta \pm$  adjusted standard error]: years to first breeding  $\sim -0.0765 \times \text{adults}[\pm 0.146] + 1.0[\pm 0.089]$ ). These results suggest that recruitment times have remained relatively constant as population size has increased. Birds that did successfully recruit tended to do so in their first or second adult year (overall mean = 1.50 years  $\pm$  1.02 SD).



**Figure 2.** Annual takahē juvenile production (as number of juveniles produced per adult) as population size increased across four islands (square = Kapiti, circle = Mana, triangle = Maud, cross = Tiritiri Matangi). Each data point represents the value for an island in a breeding season; the trend line is the fitted mean effect of adult population size using the mean age of breeders (6.3 years) and mean effect over all four islands (generalised linear regression, Table 1).

**Table 1.** Model-averaged standardised coefficients contributing to juvenile production (number of juveniles produced per adult) from 1986 to 2009, based on generalised linear modelling with a quasi-Poisson link.

Predictor <sup>1</sup>	$\beta$	Adj. SE	Lower CL	Upper CL
Intercept	-1.62	0.097	-1.81	-1.43
No. adults	-0.565	0.188	-0.933	-0.197
Mean age <sup>2</sup>	0.046	0.116	-0.182	0.273
Mana <sup>3</sup>	0.007	0.106	-0.200	0.215
Maud <sup>3</sup>	-0.054	0.143	-0.335	0.226
Tiritiri <sup>3</sup>	0.032	0.111	-0.185	0.249

<sup>1</sup>Predictors were standardised following Gelman (2008) to enable direct comparison of their magnitudes. Relative importance of predictors: no. adults = 1.0, mean age = 0.32, island = 0.21.

<sup>2</sup>Mean age is the average age of breeders across the entire population per year.

<sup>3</sup>Kapiti is the reference category.

**Table 2.** Model-averaged standardised coefficients contributing to the proportion of takahē that successfully recruited for the first time in a given year, based on generalised linear modelling with a logit link.

Predictor <sup>1</sup>	$\beta$	Adj. SE	Lower CL	Upper CL
Intercept	-0.912	0.420	-1.73	-0.0885
No. adults	-0.547	1.16	-2.82	1.72
Mana <sup>2</sup>	1.22	0.531	0.178	2.26
Maud <sup>2</sup>	0.688	0.540	-0.370	1.75
Tiritiri <sup>2</sup>	1.06	0.506	0.0678	2.05
No. adults × Mana	0.433	1.10	-1.72	2.58
No. adults × Maud	0.938	2.08	-3.13	5.01
No. adults × Tiri	0.372	1.07	-1.73	2.47

<sup>1</sup>Predictors were standardised following Gelman (2008) to enable direct comparison of their magnitudes. Relative importance of predictors: no. adults = 0.46, island = 1.00, no. adults × island interaction = 0.20.

<sup>2</sup>Kapiti Island is the reference category.

## Discussion

We observed that the proportion of breeding takahē across the islands has decreased in recent years (Fig. 1b), even despite a possible increase in the number of breeders occupying each territory, and that juvenile production has declined as total population size increased (Fig. 2). The decline in juvenile production was independent of differences between islands and the general increase in mean age of breeders. It is also unlikely to be due solely to increasing inbreeding depression, as only a weak relationship between pedigree-based inbreeding coefficients and the specific trait of juvenile production was previously observed in this population (Grueber et al. 2010).

We did not observe an effect of population density on recruitment rates (Table 2) or on time to recruitment. This may be due in part to possible confounders such as individuals recruiting onto established territories, either by offspring remaining on their natal territories beyond breeding age or increasing size of breeding groups, although support for the latter was weak. We were unable to test whether the

recruitment rates or times of Fiordland- versus island-hatched birds differed because most Fiordland-bird introductions were early in the islands' history, when the whole island population was at a relatively low density. Despite these difficulties with examining recruitment rates directly, our results (the declining proportions of breeders and juvenile production) suggest that the island population of takahē is showing signs of density dependence and that breeding capacity of the four offshore islands has been maximised.

As a consequence of the results presented here, a large number of adults with the potential to contribute to the productivity of the island population as a whole are unable to do so at present, and the proportion of adults that do contribute is decreasing (Fig. 1). If large numbers of adults remain unmated, it is likely that the implementation of recommendations to manage inbreeding and loss of genetic diversity will be impeded (Grueber & Jamieson 2008). Introducing birds with a view to increasing the genetic diversity and reducing the rate of inbreeding will be largely ineffective if new founders simply contribute to the increasing pool of non-breeding adults (i.e. those unable to establish breeding territories), although we did not detect density-dependent effects on recruitment rates per se. Of course, increasing the area of suitable breeding habitat on the islands is one possible approach for increasing carrying capacity (e.g. by habitat restoration or supplementary feeding; Komdeur 1996; Schoech et al. 2008), but due to the large territory sizes of takahē breeding pairs and their aggressive nature (Ryan & Jamieson 1998), this strategy may be limited. Therefore the best option for increasing the productivity of the island populations is to crop surplus birds and use these either to establish new island sites or to translocate back to Fiordland to augment the source population. Both of these strategies are currently being explored by the Takahē Recovery Group. The completion of pest eradication on Motutapu Island (1500 ha), in the Hauraki Gulf offshore of Auckland (P. Tisch, Takahē Recovery Group, pers. comm.), provides potential for a substantial additional sub-population, while other potential island and mainland sites are being considered. Translocation back to the source population has recently been initiated as a trial (with 13 island birds having been released in Fiordland since 2007).

In conclusion, cropping surplus birds to translocate to new sites or back to and expanding the source population in the Murchison Mountains is likely to be an effective strategy for maximising the breeding capacity of takahē on the existing islands. Cropping surplus birds will also increase the chance of recruitment by introduced birds from Fiordland when breeding sites become available, thus introducing new genetic stock to the sites to reduce mean kinship and prevent inbreeding (Grueber & Jamieson 2008).

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