

## Demography of takahe (*Porphyrio hochstetteri*) in Fiordland: environmental factors and management affect survival and breeding success

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**Abstract:** The last remaining natural population of the critically endangered takahe (*Porphyrio hochstetteri*) is confined to the Murchison Mountains in Fiordland, New Zealand. This mainland population contains about half of the c. 300 remaining takahe and benefits from one of the costliest recovery programmes in the country. Management activities include deer culling, stoat trapping, nest manipulation (e.g. removal of infertile eggs) and captive rearing of chicks. To determine what effect this intensive management has had on the recovery of the Fiordland takahe population, we modelled 25 years of survival and breeding success data as a function of environmental factors (e.g. precipitation, temperature, beech seedfall, tussock flowering) and specific management activities (egg manipulation, captive rearing, stoat control). Annual adult survival, estimated at 78% (credibility interval (CI) = 75–81%), is significantly increased to 85% (76–92% CI) in presence of stoat trapping, but is still low relative to introduced takahe populations on offshore islands and other large New Zealand bird species in predator-free environments. This suggests that the harsh environment of Fiordland may be suboptimal habitat in terms of survival for takahe. On the other hand, reproductive output in Fiordland is similar to that for introduced island populations, and is improved even further by management. Number of chicks per pair fledged with nest manipulation and captive rearing is estimated at 0.66 compared with 0.43 in the absence of nest management. The difference is explained mainly by low fledging success in the wild, especially for double clutches, which justifies the practice of removing one of two viable eggs and transferring it to a captive-rearing facility. The results of this study indicate that current management activities such as stoat trapping and captive rearing have a strong positive effect on population growth of the Murchison Mountains takahe population.

**Keywords:** captive rearing; mark–recapture; nest manipulation; New Zealand; predator control

### Introduction

The takahē (*Porphyrio hochstetteri*) is a large flightless rail endemic to New Zealand. It was widespread throughout the South Island in pre-Polynesian times, while a closely related species (*Porphyrio mantelli*), now extinct, inhabited the North Island (Trewick 1996; Trewick & Worthy 2001). The species' distribution range was reduced to Fiordland as a consequence of hunting by Māori and habitat destruction (Trewick & Worthy 2001), and by the end of the 19th century the bird was considered extinct. It was rediscovered in 1948 on the shore of Lake Orbell in the Murchison Mountains, and soon after, a 518-km<sup>2</sup> 'Special Takahe Area' was set aside for its conservation (Ballance 2001). The takahē population continued to decline after its rediscovery and reached a low of 120 individuals in 1981. As a result of intensive management of the Fiordland population and the establishment of several small offshore island populations, takahē numbers recovered to a total of 297 known individuals (168 in Fiordland) in the 2006/07 season, before dropping to about 200 (93 in Fiordland) in the 2007/08 season as a consequence of a stoat plague during the winter of 2007 (all numbers are total counts from annual surveys). About half of the takahē population resides in Fiordland, with the rest in the Burwood Bush captive rearing and breeding facility and on offshore island sanctuaries (Greaves & Joice 2007, unpubl.). The takahē is classified as 'Nationally Critical' in New Zealand's Department of Conservation threat

classification system (Hitchmough et al. 2007), while it is listed as 'Endangered' by the IUCN (2006). Conservation efforts are complicated by the fact that the remnant population is confined to a remote area of New Zealand, where any management operations are logistically difficult and costly.

Despite the relatively intact habitat in the Murchison Mountains, the Fiordland takahē population faces some major challenges, including competition for food by introduced red deer (*Cervus elaphus*) (Mills & Mark 1977; Mills et al. 1989), predation by stoats (*Mustela erminea*) (Maxwell 2001) and the severe alpine climate in a region on the periphery of its original distribution range (Maxwell & Jamieson 1997; Maxwell 2001). Although there is circumstantial evidence that stoats can kill adult takahē, so far it has not been possible to quantify the true impact of predation on the takahē population (Maxwell 2001). Takahē adult survival appears to be negatively correlated with beech seedfall (Hamilton 2005, unpubl.), which in turn is an indicator of predator plagues (King 1983). A stoat plague in 2007 caused unprecedented losses to the Fiordland takahē population, as discussed in more detail in this paper.

Current management efforts to save the takahē from extinction include deer culling, predator trapping, nest manipulation, captive rearing and relocation of birds from Fiordland to island sanctuaries free of introduced predators and food competitors. Deer culling aims at maintaining deer numbers in the Special Takahe Area below 350 animals by removing a minimum of 125 animals per year (Wickes et al.

2009). Stoat trapping has been carried out in the Murchison Mountains on and off since 1949, mostly with trap lines along valley floors, covering limited sectors of the Special Takahe Area. In 2002, a stoat control programme was initiated based on low-intensity landscape-style trapping with trap lines no more than 2 km apart, covering 15 000 ha in the south-east sector of the Murchison Mountains. This trapping programme was designed as an experiment, with the north-east sector of the Special Takahe Area set aside as a control area (Crouchley 2001, unpubl.). In 2009, the trapping programme was extended to cover the whole of the Murchison Mountains.

Nest manipulation is limited to the removal of infertile or addled eggs from nests, to encourage unsuccessful pairs to lay a second clutch, or to focus the parental investment on the remaining viable egg (Wickes et al. 2009). Additionally, eggs from wild nests are removed for captive rearing. The artificial incubation of eggs and captive rearing of chicks at Burwood Bush Takahe Rearing Unit were instigated to improve the low survival of eggs and chicks in the wild (Eason & Willans 2001). Most takahē pairs lay two eggs per clutch, but relatively few pairs are successful at raising more than one chick (Mills 1978). Second eggs from two-egg nests are thus considered surplus eggs that can be reared in captivity with only a limited loss in productivity in the wild (Mills et al. 1982, unpubl.; Mills 1990; Hamilton et al. 2006, unpubl.). Captive-reared birds are generally returned to the Murchison Mountains at one year of age. Finally, between 1984 and 1999, 25 takahē (mostly juveniles) were introduced to five small offshore islands on which predators and pests had been eradicated – primarily as a safeguard against a catastrophe striking the natural Fiordland population. Takahē on islands have bred successfully and increased to 83 adults in 2006/07 (Greaves & Joice 2007, unpubl.), although productivity per breeding pair is lower than in Fiordland (Bunin et al. 1997; Jamieson & Ryan 2001), and carrying capacity on each island is low resulting in a high incidence of inbreeding and loss of genetic diversity (Jamieson et al. 2003; Grueber & Jamieson 2008; Grueber et al. 2010).

The objective of the current study is to apply an information theoretic approach in a Bayesian framework to model takahē survival and reproductive success in the Murchison Mountains as a function of environmental factors (e.g. beech seedfall, tussock seeding, winter temperature, rain and snowfall) and specific management activities (see above). Adult survival was modelled over the period 1992/93 to 2007/08 (16 years), including a comparison of the trapped and untrapped areas. Breeding success was modelled for the period 1981–2005 (25 years), comparing manipulated and non-manipulated nests, and breeding success in the wild versus captivity. The overall aim of the study was to determine to what extent, if any, intensive management has prevented further decline in the takahē's last remaining natural population in Fiordland.

## Methods

### Field techniques

Most adult takahē in the Murchison Mountains are banded with a unique four-colour band combination, including a numbered metal band. Additionally, at any given time about 20 adult birds are fitted with a radio transmitter.

During the study period (1981–2008), the takahē population in the Murchison Mountains was surveyed twice

a year, once in October/November to search for nests and once in February/March for a chick survey. During the nest surveys, teams of two workers (occasionally accompanied by trained dogs) searched territories on foot for fresh signs of feeding and nesting. Any eggs found were candled to determine viability, and infertile or addled eggs were removed to potentially improve incubation efficiencies or to induce the pair to renest. It is assumed that the number of eggs (or egg shells) found was the actual number of eggs laid, as each nest was visited only once.

During the autumn surveys fieldworkers checked whether the nests located in spring had produced any chicks, and whether unsuccessful pairs had renested; banding of chicks was also carried out at this time. In addition to resightings of live banded birds, dead birds were occasionally recovered. All resightings and recoveries were entered in a Microsoft Access Takahe Database, held by the Department of Conservation at its Te Anau office.

### Statistical analysis – survival

Adult and juvenile survival were calculated for all wild birds in the Murchison Mountains between the 1992/93 and 2007/08 seasons, for a total of 16 years; data collected prior to 1992 were too sparse for a survival analysis. All sightings of positively identified banded birds (i.e. whose details are stored in the Takahe Database) were used, provided the age of the bird was known, as the dependence of survival on age is of interest. Birds whose first record was in the final year of the dataset (2007/08) were excluded, and any dead recoveries were kept as a resighting for the current season, provided the bird had not been dead for more than one season.

Climate data for the Murchison Mountains were also extracted for the same time period from a Microsoft Access Weather Database held by the Department of Conservation, Te Anau. The following environmental factors were included in the analysis: annual beech seedfall (seeds m<sup>-2</sup>), percentage of tussock flowering, average temperature (°C) in the three coldest months of the year, annual rainfall (mm), total rainfall (mm) during the breeding season (Oct. to Feb.), and total precipitation (mm) over winter (May to Sep.) as a proxy for snowfall. Beech seedfall and tussock flowering data were log-transformed. A bird count for the season (inclusive of all unidentified and unbanded bird sightings) was also included in the analysis, to allow for density dependence as a factor.

Multiple sightings in a year were pooled and treated as single sightings when constructing the encounter history matrix for a capture–mark–recapture (CMR) analysis. The matrix has 16 columns (one for each year) and 385 rows (one for each individual bird). For each bird, its birth-year and whether it was captive-reared or wild-raised was recorded. For each season that a bird was sighted, the following were also recorded: whether it was a chick (< 1 year of age) or an adult, whether the bird was in the stoat-trapped area (only applies from 2002 onwards), and whether the bird was wearing a radio transmitter.

A variation of the Cormack–Jolly–Seber (CJS) model for live resightings only (Cormack 1964; Jolly 1965; Seber 1965) was used to estimate takahē survival. A previous survival study on the takahē (Hegg 2006) had shown that the CJS model gives the same results as the more complex Barker model (Barker 1997) for joint recaptures and dead recoveries. Takahē survival  $S$  was modelled as:

$$\text{logit}(S) = \alpha_0 + \sum_i \alpha_i \times \text{Factor}_i + \varepsilon(t),$$

where  $\alpha_i$  are model parameters,  $Factor_i$  include age, stoat trapping and environmental variables, and  $\varepsilon(t)$  is a random error (random environmental effect), assumed to be normally distributed, with an average of zero and unknown variance. The inverse of the variance was drawn from a gamma distribution with both hyperparameters set to 0.01.

One of the assumptions of the CJS model is that the probability of sighting is the same for all birds; this assumption is likely to be violated in the case of the takahē, as some birds are fitted with radio transmitters, and the survey effort varied in different sectors of the Murchison Mountains due to unequal terrain and ease of access. To account for this heterogeneity, the probability of resighting  $p$  was modelled as:

$$\text{logit}(p) = \beta_1 + \beta_2 \times Tx + \beta_3 \times Captive + \beta_4 \times f_s,$$

where  $Tx$  takes a value of 1 if a bird was wearing a radio transmitter, 0 otherwise;  $Captive$  takes a value of 1 if a bird was captive-reared in Burwood, 0 otherwise; and

$$f_s = \frac{N_{seasons}}{Y_L - Y_F + 1}$$

( $f_s$  stands for 'frequency of sighting'), where  $N_{seasons}$  is the number of seasons a bird was sighted,  $Y_L$  is the year when a bird was last sighted, and  $Y_F$  is the year when a bird was first sighted.

WinBUGS 1.4.1 (Lunn et al. 2000), a software for developing models in a Bayesian framework, was used for model selection and parameter estimation; all models were written by the authors. The best model was selected according to the DIC criterion (Spiegelhalter et al. 2002). When coding models in WinBUGS, all environmental factors were standardised to a mean of zero and a standard deviation of 1. Normal distributions with a mean of zero and a large variance (10) were selected as semi-informative prior distributions for all  $\alpha$  and  $\beta$  parameters, unless the model failed to converge, in which case we reduced the variance to 2 or smaller (the variance, however, was the same for all models in a set). All models were run with two Markov chains and 100 000 iterations, and an additional 5000 burn-ins per chain. Convergence was checked by plotting the parameter history, and a visual confirmation that the parameter estimate had stabilised after the burn-in phase.

### Statistical analysis – breeding success

Breeding success is usually calculated as the overall number of chicks fledged per pair each year, or as a combination of hatching (number of eggs hatched per pair) and fledging success (number of chicks fledged per egg hatched per year). In the case of the takahē, nest management depends on clutch size and egg viability. A more detailed analysis including egg fertility and clutch size is therefore warranted. The following steps in the breeding process of the takahē were analysed: probability of a pair nesting, probability of reneating given the failure of the first-clutch nest (dependent on whether the nest failure happened during incubation or after hatching), clutch size (different for first- and second-clutch nests), egg viability (dependent on clutch size), hatching success in the wild (dependent on clutch size and on nest management), fledging success in the wild (dependent on clutch size and on nest management), hatching and fledging success in captivity.

Breeding success in the wild was analysed using all the data collected during nest surveys in the Murchison Mountains between the 1981/82 and 2005/06 field seasons (totalling

25 seasons). Breeding success in captivity was analysed using 10 years of data, collected between the 1996/07 and 2005/06 seasons and stored in the Takahe Database. The same environmental factors were included as in the survival analysis.

A previous study had found that stoat trapping has no effect on takahē breeding success (Hegg 2006), while a field study on takahē egg and chick mortality over a 4-year period had failed to detect any evidence of stoat predation on takahē nests (Maxwell & Christie 2005, unpubl.). Stoat trapping was therefore not included in the breeding success analysis.

Whether a pair nests and reneats, egg viability, hatching success and fledging success of single clutches are discrete variables with a binary outcome: success (1) or failure (0) (e.g. nested / did not nest, hatched / did not hatch). The following equation was used to calculate the probability of success,  $P_{Success}$ , for each year of the study:

$$N_{Success} \sim \text{Binomial}(P_{Success}, N),$$

where  $N$  is the number of trials for the year (e.g. total number of pairs, total number of eggs), and  $N_{Success}$  is the number of successful events (e.g. number of pairs that nested, number of eggs that hatched). The probability of success was modelled as

$$\text{logit}(P_{Success}) = \alpha_0 + \sum_i \alpha_i \times Factor_i + \varepsilon(t),$$

where  $\alpha_i$  are model parameters,  $Factor_i$  are independent factors including the standardised environmental variables, and  $\varepsilon(t)$  is a random error, assumed to be normally distributed, with an average of zero and unknown variance. A detailed description of  $N$ ,  $N_{Success}$  and  $Factor_i$  for each step in the breeding process is provided in Table 1.

Clutch size is an event with three possible outcomes: one egg, two eggs or three eggs. Viability, hatching success and fledging success of two-egg nests also have three possible outcomes: complete failure, one successful egg/chick out of two, or two successful eggs/chicks. The following equation was used to calculate the probability of an outcome  $i$ ,  $P_i$  for each year of the study:

$$N_i \sim \text{Multinomial}(P_i, N_{Trials}),$$

where  $N_{Trials}$  is the number of trials for the year and  $N_i$  is the number of events with outcome  $i$ . The probability of an outcome  $i$  was modelled as:

$$\text{logit}(P_i) = \alpha_{0,i} + \sum_k \alpha_{k,i} \times Factor_k + \varepsilon(t),$$

with the equation variables taking the same form as given above (for details see Table 2).

The above binomial and multinomial equations were coded in WinBUGS 1.4.1, with all aspects of modelling (number of Markov chains, burn-ins and repetitions; prior distributions) being the same as for the survival analysis. The best model was selected according to the DIC criterion. Throughout the results, parameter estimates are followed by credibility intervals (CI).

## Results

### Survival analysis

Life histories were compiled for 385 individual birds, spanning a period of 16 years (1992/93 to 2007/08) and adding up to a

**Table 1.** Descriptors for binomial equations for analysis of takahē (*Porphyrio hochstetteri*) breeding success in the Murchison Mountains, Fiordland, New Zealand.

Demographic parameter	Trials ( $N$ ) <sup>1</sup>	Successful events ( $N_{Success}$ )	Factors
Probability of nesting	Total number of territorial pairs	First-clutch nests with eggs ( $N$ )	Environment
Probability of re-nesting	First-clutch nests known to have failed. [Includes nests that had eggs removed/transferred.] ( $N$ )	Second-clutch nests ( $N$ )	Environment; nest failure during egg- or chick-stage
Viability of one-egg nests	One-egg nests ( $N$ )	Viable eggs <sup>2</sup> ( $N$ )	Environment
Hatching success of one-egg nests	Nests with one viable egg ( $N$ )	Eggs that hatched ( $N$ )	Environment; nest managed (transferred egg); two-egg nest with one dud egg removed
Fledging success of one-egg nests	Nests that hatched one chick ( $N$ )	Chicks surviving to > 30 days ( $N$ )	Environment; nest managed (transferred egg/chick); two-egg nest that had one dud egg removed
Hatching success <sup>3</sup>	Eggs transferred to Burwood ( $N$ )	Chicks hatched ( $N$ )	-
Fledging success <sup>3</sup>	Chicks hatched/transferred to Burwood ( $N$ )	Chicks fledged ( $N$ )	-
Survival over first winter <sup>3</sup>	Chicks fledged in Burwood ( $N$ )	Juveniles released into Murchison Mts ( $N$ )	-

<sup>1</sup>Based on nests where viability of eggs and fate of nests are known.

<sup>2</sup>Non-viable eggs were infertile, addled, broken or contained dead embryos.

<sup>3</sup>In Burwood Captive Rearing Unit.

**Table 2.** Descriptors for multinomial equations for analysis of environmental factors affecting takahē (*Porphyrio hochstetteri*) breeding success in the Murchison Mountains, Fiordland, New Zealand.

Demographic parameter	Trials ( $N_{Trial}$ ) <sup>1</sup>	Events with outcome $i$ ( $N_i$ )
Size of first <sup>1</sup> clutch	First-clutch nests ( $N$ )	Nests with 1, 2 or 3 eggs ( $N$ )
Size of second clutch	Second-clutch nests ( $N$ )	Nests with 1, 2 or 3 eggs ( $N$ )
Viability of two-egg nests	Two-egg nests <sup>2</sup> ( $N$ )	Nests with 0, 1 or 2 viable eggs <sup>3</sup> ( $N$ )
Hatching success of two-egg nests	Nests with two viable eggs <sup>3</sup> ( $N$ )	Nests that hatched 0, 1 or 2 chicks ( $N$ )
Fledging success of two-chick nests	Nests with two chicks ( $N$ )	Nests with 0, 1 or 2 chicks surviving to > 30 days ( $N$ )

<sup>1</sup>Based on nests where viability of eggs and fate of nest are known.

<sup>2</sup>Three-egg nests were pooled with two-egg nests. They represent 2% of first clutches and are thus too rare to warrant a separate analysis. Three-egg nests with three viable eggs are extremely rare (<1%).

<sup>3</sup>Non-viable eggs were infertile, addled, broken or contained dead embryos.

total of 1127 useful sightings (including 83 dead recoveries). Of 385 birds, 60 were sighted in the stoat trapping area since the start of the stoat trapping programme in 2002; the remaining 325 birds were either seen outside the trapped area or were last resighted before the trapping programme started. In addition, 212 birds were captive-reared and 173 birds were wild-reared.

Eighty-six birds in the dataset were fitted with a radio transmitter (24 in the stoat trapping area), for a total of 358 useful sightings over a period of 16 years. Of these 86 birds, 37 were recovered dead (11 of these in the 2007/08 season). Fifteen birds had the transmitter removed or were resighted with a failed transmitter ( $2.6 \pm 3.0$  SD years after fitting the transmitter), seven are known alive at present, and the

remaining 27 were lost track of ( $4.0 \pm 3.8$  SD years after fitting the transmitter).

The survival model that scored the lowest DIC is a model where takahē survival depends on a quadratic effect of age, an effect of stoat trapping, and an effect of beech seedfall, tussock flowering, winter temperature, rainfall and snowfall, as well as a random time effect (Table 3). It is worth noting that the top seven models each had a  $\Delta\text{DIC} < 1$ . All these models included an age and a random time effect, as well as stoat trapping, indicating a high level of confidence in the importance of these three factors relative to the variation in annual survival. All seven models give consistent results, the only difference being in the removal of factors with the highest level of uncertainty in the top ranked model. All values of  $\alpha$

**Table 3.** Survival (S) and resight (p) models for takahē (*Porphyrio hochstetteri*) in the Murchison Mountains, Fiordland, New Zealand, 1992–2008, ranked according to lowest Deviance Information Criterion (DIC). (Table shows a subset of the models run only; see text for further details.)

Model	pD <sup>1</sup>	DIC	ΔDIC
1 Logit(S) = $\alpha_1 + \text{Adult} \cdot (\alpha_2 + \alpha_3 \cdot \text{Age} + \alpha_4 \cdot \text{Age}^2) + \alpha_5 \cdot \text{Trapped} + \alpha_6 \cdot \text{Seedfall} + \alpha_7 \cdot \text{Tussock} + \alpha_8 \cdot \text{Temperature} + \alpha_9 \cdot \text{Rain} + \alpha_{10} \cdot \text{Snow} + \varepsilon(t)$ Logit(p) = $\beta_1 + \beta_2 \cdot \text{Tx} + \beta_3 \cdot \text{FrequencyOfSighting}$	20.09	1593.66	
2 Logit(S) = $\alpha_1 + \text{Adult} \cdot (\alpha_2 + \alpha_3 \cdot \text{Age} + \alpha_4 \cdot \text{Age}^2) + \alpha_5 \cdot \text{Trapped} + \alpha_6 \cdot \text{Seedfall} + \alpha_7 \cdot \text{Temperature} + \alpha_8 \cdot \text{Rain} + \alpha_9 \cdot \text{Snow} + \varepsilon(t)$ Logit(p) = $\beta_1 + \beta_2 \cdot \text{Tx} + \beta_3 \cdot \text{FrequencyOfSighting}$	20.06	1593.98	0.32
3 Logit(S) = $\alpha_1 + \text{Adult} \cdot (\alpha_2 + \alpha_3 \cdot \text{Age} + \alpha_4 \cdot \text{Age}^2) + \alpha_5 \cdot \text{Trapped} + \alpha_6 \cdot \text{Seedfall} + \alpha_7 \cdot \text{Tussock} + \alpha_8 \cdot \text{Rain} + \alpha_9 \cdot \text{Snow} + \varepsilon(t)$ Logit(p) = $\beta_1 + \beta_2 \cdot \text{Tx} + \beta_3 \cdot \text{FrequencyOfSighting}$	20.14	1593.99	0.33
4 Logit(S) = $\alpha_1 + \text{Adult} \cdot (\alpha_2 + \alpha_3 \cdot \text{Age} + \alpha_4 \cdot \text{Age}^2) + \alpha_5 \cdot \text{Trapped} + \alpha_6 \cdot \text{Seedfall} + \alpha_7 \cdot \text{Tussock} + \alpha_8 \cdot \text{Temperature} + \alpha_9 \cdot \text{Rain} + \alpha_{10} \cdot \text{Snow} + \varepsilon(t)$ Logit(p) = $\beta_1 + \beta_2 \cdot \text{FrequencyOfSighting}$	19.17	1594.01	0.35
5 Logit(S) = $\alpha_1 + \text{Adult} \cdot (\alpha_2 + \alpha_3 \cdot \text{Age} + \alpha_4 \cdot \text{Age}^2) + \alpha_5 \cdot \text{Trapped} + \alpha_6 \cdot \text{Tussock} + \alpha_7 \cdot \text{Temperature} + \alpha_8 \cdot \text{Rain} + \alpha_9 \cdot \text{Snow} + \varepsilon(t)$ Logit(p) = $\beta_1 + \beta_2 \cdot \text{Tx} + \beta_3 \cdot \text{FrequencyOfSighting}$	20.27	1594.06	0.40
6 Logit(S) = $\alpha_1 + \text{Adult} \cdot (\alpha_2 + \alpha_3 \cdot \text{Age} + \alpha_4 \cdot \text{Age}^2) + \alpha_5 \cdot \text{Trapped} + \alpha_6 \cdot \text{Seedfall} + \alpha_7 \cdot \text{Tussock} + \alpha_8 \cdot \text{Temperature} + \alpha_9 \cdot \text{Snow} + \varepsilon(t)$ Logit(p) = $\beta_1 + \beta_2 \cdot \text{Tx} + \beta_3 \cdot \text{FrequencyOfSighting}$	20.16	1594.21	0.55
7 Logit(S) = $\alpha_1 + \text{Adult} \cdot (\alpha_2 + \alpha_3 \cdot \text{Age} + \alpha_4 \cdot \text{Age}^2) + \alpha_5 \cdot \text{Trapped} + \alpha_6 \cdot \text{Seedfall} + \alpha_7 \cdot \text{Tussock} + \alpha_8 \cdot \text{Temperature} + \alpha_9 \cdot \text{Rain} + \varepsilon(t)$ Logit(p) = $\beta_1 + \beta_2 \cdot \text{Tx} + \beta_3 \cdot \text{FrequencyOfSighting}$	20.32	1594.38	0.72
8 Logit(S) = $\alpha_1 + \text{Adult} \cdot (\alpha_2 + \alpha_3 \cdot \text{Age} + \alpha_4 \cdot \text{Age}^2) + \alpha_5 \cdot \text{Seedfall} + \alpha_6 \cdot \text{Tussock} + \alpha_7 \cdot \text{Temperature} + \alpha_8 \cdot \text{Rain} + \alpha_9 \cdot \text{Snow} + \varepsilon(t)$ Logit(p) = $\beta_1 + \beta_2 \cdot \text{Tx} + \beta_3 \cdot \text{FrequencyOfSighting}$	19.13	1595.09	1.43
9 Logit(S) = $\alpha_1 + \text{Adult} \cdot (\alpha_2 + \alpha_3 \cdot \text{Age} + \alpha_4 \cdot \text{Age}^2) + \alpha_5 \cdot \text{Trapped} + \alpha_6 \cdot \text{Seedfall} + \alpha_7 \cdot \text{Tussock} + \alpha_8 \cdot \text{Temperature} + \alpha_9 \cdot \text{Rain} + \alpha_{10} \cdot \text{Snow} + \varepsilon(t)$ Logit(p) = $\beta_1 + \beta_2 \cdot \text{Tx} + \beta_3 \cdot \text{CaptiveReared} + \beta_4 \cdot \text{FrequencyOfSighting}$	21.02	1595.42	1.76
10 Logit(S) = $\alpha_1 + \text{Adult} \cdot (\alpha_2 + \alpha_3 \cdot \text{Age} + \alpha_4 \cdot \text{Age}^2) + \alpha_5 \cdot \text{Trapped} + \alpha_6 \cdot \text{Seedfall} + \alpha_7 \cdot \text{Tussock} + \alpha_8 \cdot \text{Temperature} + \alpha_9 \cdot \text{Rain} + \alpha_{10} \cdot \text{Snow} + \varepsilon(t)$ Logit(p) = $\beta_1 + \beta_2 \cdot \text{CaptiveReared} + \beta_3 \cdot \text{FrequencyOfSighting}$	20.28	1596.09	2.43
11 Logit(S) = $\alpha_1 + \text{Adult} \cdot (\alpha_2 + \alpha_3 \cdot \text{Age} + \alpha_4 \cdot \text{Age}^2) + \alpha_5 \cdot \text{Trapped} + \alpha_6 \cdot \text{Seedfall} + \alpha_7 \cdot \text{Tussock} + \alpha_8 \cdot \text{Temperature} + \alpha_9 \cdot \text{Rain} + \alpha_{10} \cdot \text{Snow} + \varepsilon(t)$ Logit(p) = $\beta_1 + \beta_2 \cdot \text{Tx} + \varepsilon(\text{bird})$	128.19	1631.27	37.61
12 Logit(S) = $\alpha_1 + \text{Adult} \cdot (\alpha_2 + \alpha_3 \cdot \text{Age} + \alpha_4 \cdot \text{Age}^2) + \alpha_5 \cdot \text{Trapped} + \alpha_6 \cdot \text{Seedfall} + \alpha_7 \cdot \text{Tussock} + \alpha_8 \cdot \text{Temperature} + \alpha_9 \cdot \text{Rain} + \alpha_{10} \cdot \text{Snow} + \varepsilon(t)$ Logit(p) = $\beta_1 + \beta_2 \cdot \text{Tx} + \beta_3 \cdot \text{CaptiveReared}$	19.20	1845.27	251.61
13 Logit(S) = $\alpha_1 + \text{Adult} \cdot (\alpha_2 + \alpha_3 \cdot \text{Age} + \alpha_4 \cdot \text{Age}^2) + \alpha_5 \cdot \text{Trapped} + \alpha_6 \cdot \text{Seedfall} + \alpha_7 \cdot \text{Tussock} + \alpha_8 \cdot \text{Temperature} + \alpha_9 \cdot \text{Rain} + \alpha_{10} \cdot \text{Snow} + \varepsilon(t)$ Logit(p) = $\beta_1 + \beta_2 \cdot \text{Tx}$	18.68	1869.82	276.16
14 Logit(S) = $\alpha_1 + \text{Adult} \cdot (\alpha_2 + \alpha_3 \cdot \text{Age} + \alpha_4 \cdot \text{Age}^2) + \alpha_5 \cdot \text{Trapped} + \alpha_6 \cdot \text{Seedfall} + \alpha_7 \cdot \text{Tussock} + \alpha_8 \cdot \text{Temperature} + \alpha_9 \cdot \text{Rain} + \alpha_{10} \cdot \text{Snow} + \varepsilon(t)$ Logit(p) = $\beta_1$	17.65	1891.12	297.46

<sup>1</sup>pD = effective dimension

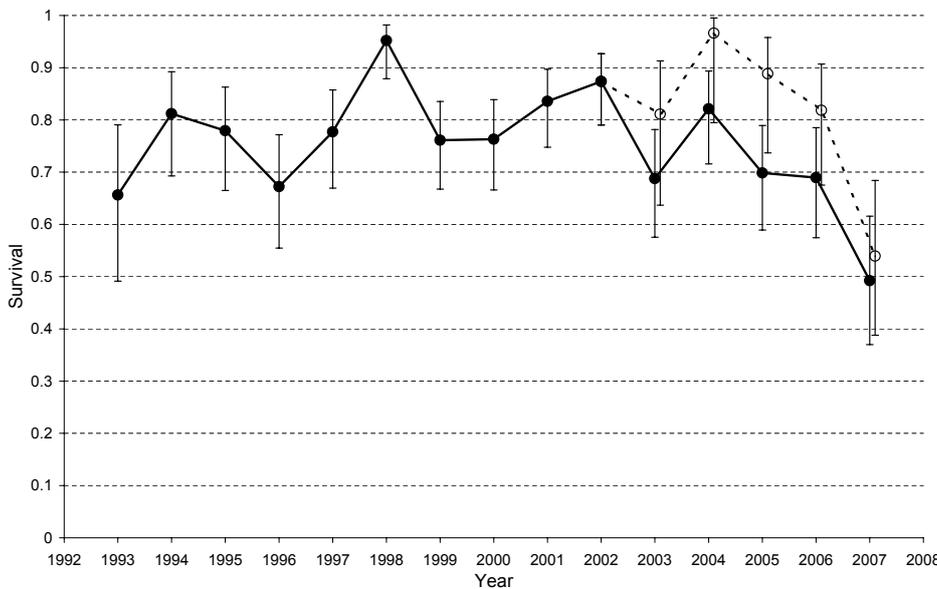
and  $\beta$  (and their standard deviations) are very similar among the top 10 models.

The average survival rates (best model only) for the entire period of 1992–2008 are summarised in Table 4 and Fig. 1, while the values of the parameters  $\alpha_1$  to  $\alpha_{10}$  are reported in Table 5. Survival depends on age (Fig. 2), and is higher in the trapped area than in the untrapped area ( $P = 98.2\%$ , where  $P$  is the probability that the effect is greater than zero) (Fig. 1). The effectiveness of stoat trapping appeared to be reduced during the last mast season, with an estimated survival rate of only 54% (39–68% CI) in the trapped area, versus 49% (37–62% CI) in the untrapped area. Survival is also positively affected by warm winters ( $P = 79\%$ ) and high rainfall ( $P = 91\%$ ), while it is negatively affected by beech mast events in the previous year ( $P = 86\%$ ) and high snowfall ( $P = 94\%$ ) (Table 5). The mean probability of resighting is 82% (77–86% CI) for birds fitted with radio transmitters and 67% (64–71% CI) for birds without a transmitter. The model fit is greatly improved if ‘frequency of sighting’ is added to the equation of the probability of resighting (Table 3).

**Breeding success analysis**

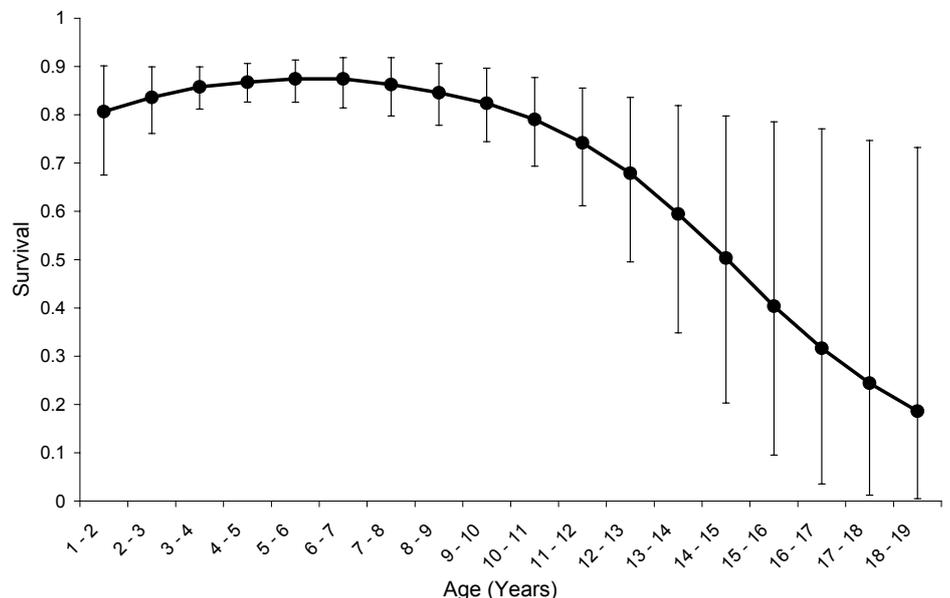
The results of the breeding success analysis, inclusive of sample size and effect of environmental factors, are summarised in Tables 6 and 7, while the model selection results are found in Appendix 1. It is immediately obvious that the fledging success in captivity (87%, 79–92% CI) is substantially higher than in the wild (37%, 31–43% CI for unmanaged one-egg nests and two-egg nests; 57%, 48–66% CI for managed nests). This results in an overall productivity that is substantially higher for managed nests (chicks per pair = 0.66 on average) than for unmanaged nests (0.43) (Table 7).

Environmental factors also affect breeding success, especially cold winters (lower probability of reneating and lower egg viability), summer rainfall (lower hatching success), and tussock flowering (increased probability of reneating and increased size of second clutches) (Table 6). The probability of reneating and egg viability also appear to be lower at high population densities (Table 6), but this result is confounded by a positive correlation between population density and winter temperature during the study period.



**Figure 1.** Takahē (*Porphyrio hochstetteri*) adult survival in the Murchison Mountains, Fiordland, New Zealand, 1992–2007, in the untrapped area (solid line with black circles) and in the stoat trapping area (dash line with white circles). The current stoat trapping programme started in 2002. Survival is over one year, e.g. the 2007 value indicates survival between the 2006/07 breeding season and the 2007/08 breeding season. Bars represent 95% credibility intervals.

**Figure 2.** Takahē (*Porphyrio hochstetteri*) adult survival rate as a function of age based on birds fitted with radio transmitters only, for Murchison Mountains, Fiordland, New Zealand, 1992–2007. Bars represent 95% credibility intervals.



**Table 4.** Annual survival of juvenile and adult takahē (*Porphyrio hochstetteri*) in untrapped and trapped areas of the Murchison Mountains, Fiordland, New Zealand, 1992–2008. SD = standard deviation; CI = 95% credibility interval. (Parameter estimates shown are for the best model only; see Table 3.)

		Mean	SD	95% CI	
		(%)	(%)	2.5%	97.5%
Untrapped area	Chicks	75	4.0	67	83
	Adults	78	1.5	75	81
Stoat trapping area	Chicks	83	4.3	75	91
	Adults	85	3.3	76	92

**Table 5.** Logistic regression parameters for survival and resighting probability for takahē (*Porphyrio hochstetteri*) in the Murchison Mountains, 1992–2008 ( $N = 385$ ). SD = standard deviation; CI = 95% credibility interval; P = probability that the parameter of interest is different from zero.

		Model parameter	Mean	SD	95% CI		P > 0
					2.5%	97.5%	(%)
Survival probability	$\alpha_1$ – Chick survival		1.06	0.32	0.43	1.71	-
	$\alpha_2$ – Adult survival		-1.06	0.32	-1.66	-0.45	-
	$\alpha_3$ – Age, linear term		0.54	0.12	0.33	0.77	-
	$\alpha_4$ – Age, quadratic term		-0.035	0.010	-0.055	-0.016	-
	$\alpha_5$ – Stoat trapping		0.59	0.34	-0.05	1.26	98
	$\alpha_6$ – Beech seedfall		-0.34	0.30	-0.93	0.22	14
	$\alpha_7$ – Tussock flowering		-0.09	0.34	-0.79	0.56	38
	$\alpha_8$ – Winter temperature		0.26	0.30	-0.34	0.87	79
	$\alpha_9$ – Total rainfall		0.55	0.39	-0.16	1.33	91
	$\alpha_{10}$ – Snowfall		-0.68	0.41	-1.55	0.14	6
Resighting probability	$\beta_1$ – Constant		-3.97	0.40	-4.81	-3.20	-
	$\beta_2$ – Radio transmitter		0.42	0.27	-0.11	0.96	-
	$\beta_3$ – Frequency of sighting		6.68	0.53	5.65	7.80	-

## Discussion

### Survival

Our results indicate that takahē survival is affected by predator trapping, environmental variables and age, each of which is discussed in turn below. There is strong evidence that, since the start of the stoat trapping programme, takahē annual survival in the trapped area (85%, 76–92% CI) has been higher than in the untrapped area (78%, 75–81% CI). The difference is not only statistically significant (i.e. there is a 98% probability that adult survival is increased by stoat trapping) but biologically important, with mortality in the trapped area reduced by 30% in non-mast years. This result strongly supports the recent decision to extend the trapping programme to the whole of the Murchison Mountains, as well as the current practice of running the trap lines during both mast years and non-mast years.

Takahē survival during the 2007/08 season was the lowest on record since the start of systematic surveys in the Murchison Mountains in 1981. A stoat plague of unprecedented magnitude was triggered by a combination of events including a large beech mast followed by a warm summer, which resulted in unusually high rat numbers (Greaves et al. 2008, unpubl.). The rat population crashed during the next winter, which may have caused stoats to switch prey. Since this is the first time such a crash of the takahē population has been observed, we do not

have sufficient information to estimate the frequency of similar events. The benefit of the stoat trapping programme appeared to be only minor during the stoat plague, suggesting that stoats were able to quickly reinvade the trapped area. At the same time, more recent surveys have indicated greater numbers of takahē than expected in the trapped area (Greaves et al. 2008), suggesting that our calculated value of 54% for the survival rate in the trapped area during 2007/08 is an underestimate. The stoat plague coincided with the last year in the analysis, when the estimates of the survival rate and of the resighting rate in a mark–recapture model are confounded. We recommend that the survival analysis should be repeated to include resightings from at least two more seasons, to confirm whether the low survival during 2007/08 in the trapped area is real, or an artefact caused by a lower resighting rate. Either way, we expect that the impact of similar events will be reduced after the recent extension of the trapping programme from 15 000 ha to 50 000 ha, as immigration of stoats will most likely affect the periphery rather than the entire trapped area.

Even with predator trapping, takahē survival in Fiordland appears to be lower than on offshore islands (94%; Bunin et al. 1997). While stoat trapping will reduce rather than eliminate predation, we suggest that introduced mammals are not the only reason for the high takahē mortality in Fiordland. Also important is the fact that the Murchison Mountains are at the extreme end of the takahē's former range (Gray & Craig 1991),

**Table 6.** Breeding success parameters for takahē (*Porphyrio hochstetteri*) in the Murchison Mountains (1981–2005) and in Burwood Captive-rearing Unit (1996–2005), New Zealand. CI = 95% credibility interval; SD = standard deviation; *N* = sample size; effect (positive (+) or negative (–)) of environmental factors; *P* = probability that the effect of environmental factor is different from zero (calculated for binomial events only).

Demographic parameter	Mean and (CI) (%)	SD (%)	<i>N</i>	Environmental effects (+/-)	<i>P</i> > 0 (%)
Probability of nesting	76 (73–78)	1.5	1286	Beech seedfall (–)	22.9
Probability of renesting				Population density (–)	99.7
Nest failed in egg stage	22 (18–27)	1.5	455	Tussock seeding (+)	99.4
Nest failed in chick stage	10 (7–157)	1.7	228	Winter temperature (+)	>99.9
				Snowfall (–)	98.9
Size of first clutch			951		
1 egg	35 (33–39)	1.5			
2 eggs	63 (59–65)	1.6			
3 eggs	2 (1–4)	0.5			
Size of second clutch			140	Tussock (+)	-
1 egg	57 (49–64)	3.9			
2 eggs	39 (32–47)	3.9			
3 eggs	4 (2–8)	1.5			
Viability of one-egg nests	83 (79–87)	1.9	380		
Viability of two-egg nests			585	Population density (–)	-
0 viable eggs	15 (12–18)	1.4		Winter temperature (+)	-
1 viable egg	26 (22–30)	1.9			
2 viable eggs	59 (55–63)	2.0			
Hatching success one-egg nests					
Unmanaged	94 (91–96)	1.4	283		
2 eggs, 1 to Burwood	93 (88–97)	2.3	135		
2 eggs, 1 dud removed	88 (83–92)	2.7	138		
Hatching success two-egg nests			102	Summer rain (–)	-
0 eggs hatched	8 (3–14)	2.8			
1 egg hatched	16 (9–24)	3.8			
2 eggs hatched	77 (67–85)	4.5			
Fledging success one-chick nests					
Unmanaged	37 (31–43)	3.0	258		
2 chicks, 1 to Burwood	51 (42–59)	4.4	130		
2 eggs, 1 dud removed	57 (48–66)	4.6	115		
Fledging success two-chick nests			75		
0 chicks fledged	45 (37–56)	4.8			
1 chick fledged	34 (25–41)	4.2			
2 chicks fledged	21 (12–30)	4.5			
Burwood hatching success	83 (70–86)	4.0	80		
Burwood fledging success	87 (79–92)	3.1	107		
Burwood survival first winter	90 (83–94)	3.0	92		

**Table 7.** Takahē (*Porphyrio hochstetteri*) productivity per nesting pair in the Murchison Mountains, Fiordland, New Zealand, 1981–2005.

Productivity parameter	First clutch	Second clutch	Total
Eggs laid per pair	1.69	0.13	1.82
Eggs viable per pair	1.24	0.09	1.34
Eggs hatched per pair	1.09	0.08	1.18
Chicks fledged per pair (without captive rearing)	0.40	0.03	0.43
Chicks fledged per pair (with captive rearing)	0.35 + 0.28 <sup>1</sup>	0.03	0.66
Failed nests per pair	0.55		
Renests per pair	0.09		

<sup>1</sup>Contribution of captive rearing programme in Burwood Captive-rearing Unit.

with cold temperatures, thick snow-cover and avalanches during the winter season all taking their toll (Maxwell & Jamieson 1997; Maxwell 2001). In pre-Polynesian times takahē were distributed across most lowland regions in the eastern part of the South Island (Trewick & Worthy 2001), and it is likely that survival rates would have been higher there than they are in mountainous Fiordland. The survival rates of most other large New Zealand bird species in protected areas are also generally higher: 91.8% for the brown kiwi *Apteryx mantelli* and 89.3% for the great spotted kiwi *Apteryx haastii* (McLennan et al. 1996) and 96% for the North Island kōkako *Callaeas cinerea wilsoni* (Basse et al. 2003). Because adult takahē are herbivorous and require large home ranges and breeding territories, suitable large sites containing sufficient grasses and sedges and few or no introduced predators do not currently exist outside the Murchison Mountains (Jamieson & Ryan 2001).

We found that takahē adult survival is lower in seasons following beech mast years, a result that is consistent with the findings of a previous study (Hamilton 2005, unpubl.). This negative correlation has a moderate level of confidence ( $P = 86\%$ ), but is biologically important, with mortality rate following beech mast years (which are associated with stoat eruptions) being about twice as high as in normal years. This adds one more piece of evidence that stoat predation on adult takahē is significant, even though direct observations are scarce.

Cold winters and high snowfall were shown to have a negative effect on takahē survival (see Maxwell 2001). The effect of lower winter temperature translates to an increase in mortality by 15–20% for every degree Celsius difference in the mean temperature over the three coldest months, with a moderate level of confidence (79%) that the negative correlation is real. The effect of snowfall appears to be more important, with a 50% increase in mortality for every additional metre of snow ( $P = 94\%$ ). In cold winters, frozen ground will make it difficult for takahē to grub fern rhizomes, and heavy frosts can kill young plants that otherwise would provide food for the birds. A high snowfall impedes foraging as it covers the vegetation, and increases the risk of avalanches (Maxwell 2001). It is also possible that cold winters and high snowfall cause an increase of predation by stoats on takahē as other preys (mainly rats and mice) become scarce.

The beneficial effect of a high annual rainfall on takahē survival is more difficult to explain. It is possible that rainfall assists snow melt in spring, and increases food availability by enhancing vegetation growth. It is also possible that the effect of rainfall is an artefact: snowfall and rainfall are positively correlated, and if the best model overestimates the negative effect of snowfall, it would compensate for this with an (apparent) positive effect of rainfall. Taken together, a significant effect of rainfall on takahē survival should be viewed with caution.

Our results also provide good evidence for a quadratic effect of age on takahē survival, with survival rates being maximum (above 80%) between 3 and 11 years of age, then declining substantially under the effect of senescence after 12 years of age. The probability that a bird will survive to the next breeding season is about 70% for a 12-year-old bird, 50% for a 14-year-old bird, and only 20% for an 18-year-old bird. An analogous pattern has been described for a number of bird species, including great skuas *Catharacta skua* (Ratcliffe et al. 2002) and black-legged kittiwakes *Rissa tridactyla* (Frederiksen et al. 2004).

The higher resighting rate of 82% (77–86% CI) for birds fitted with radio transmitter versus 67% (64–71% CI) for those without is not surprising. However, the vastly improved model fit when the frequency of sighting is included in the model indicates that radio transmitters are not the only source of heterogeneity in the probability of resighting. Individual bird habits and an unequal survey effort in different sectors of the Murchison Mountains are also likely to play an important role, yet are too complex to model.

### Breeding success

The takahē reproductive output from unmanaged nests in the Murchison Mountains is 0.43 (chicks at 30 days of age) per breeding pair. Considering that only about two-thirds of the chicks survive to breeding age, a takahē pair would need to breed for seven or eight seasons to replace themselves. In comparison, the reproductive output of takahē on islands was estimated at 0.57 per pair (Jamieson & Ryan 2001), although it has dropped to 0.49 in the last decade (data from Island Takahē SPARK database, Department of Zoology, University of Otago) as the islands have reached carrying capacity and birds have become more inbred (Grueber et al. 2010).

With nest management (removal of one viable egg from two egg clutches) the reproductive output of chicks in the wild drops to 0.38 per pair. This is a slight decrease caused by the removal of viable eggs, but is partially compensated by the higher fledging success of single clutches. Chicks raised in captivity at Burwood and returned to the Murchison Mountains greatly improve overall productivity of managed nests to 0.66 per pair. This implies that nest management, combined with the captive-rearing programme, increases the takahē's reproductive output by almost 55%, and explains the slow but significant growth in the wild takahē population since 1993 when captive-reared birds were first returned to the Murchison Mountains (Hegg 2007).

There is a caveat to the above observation – the low productivity of 0.43 per pair is under the scenario of no management yet still under the effect of human disturbance, as nests are visited and eggs are measured and candled. If reproductive success in the absence of human disturbance were higher, the advantage of management would be smaller than the numbers above suggest. When setting up the stoat trapping experiment, a small 'minimum disturbance area' was set aside in the Murchison Mountains to assess takahē reproductive success under minimum human disturbance, including predator control. A recent analysis of breeding success data in the minimum disturbance area suggests that nest manipulation has a negligible effect on takahē reproductive output (Maxwell 2010, unpubl.).

On average, 75% (73–78% CI) of the takahē pairs found in the Murchison Mountains in any given year nest and lay eggs. If we take the distribution of the age at first reproduction (based on data from island birds) and multiply it by the stable age distribution for the takahē population (Hegg 2007), we estimate that 77% of all adult birds are ready to nest in any given year. This strongly suggests that the 25% of pairs that are not nesting are young pairs (mostly 2 or 3 years of age) that will breed eventually once they have reached maturity.

Pairs are twice as likely to re-nest if the first clutch failed in the egg stage rather than in the chick stage. The probability of a pair re-nesting is about 50% higher in tussock seeding years ( $P = 99.4\%$ ), because of the high quantity and quality of available food. Not only can adult takahē get higher nutrition from the tussock tillers, but insect numbers are also bound to

be higher (McKone et al. 2001), and insects are an important component of takahē chick diet during the first few weeks after hatching. The re-nesting rate is higher than average in years of low snowfall ( $P = 98.9\%$ ) and after warm winters ( $P > 99.9\%$ ); the latter effect is especially important, with a 70% increase in the probability of re-nesting for every degree Celsius difference in mean winter temperature. This is because breeding birds are likely to be in better condition, and are able to start breeding earlier.

The first clutch in the season is typically two eggs, the ratio of two-egg clutches to one-egg clutches being about 2:1. For re-nests, the ratio is inverted, which is not surprising given that many bird species lay smaller clutches late in the nesting season (Loman 1982; Sheldon et al. 2003; Gil-Delgado et al. 2005). The probability of a second nest having two eggs doubles from 40% to 80% in tussock flowering years. Tussock masts only affect the size of second clutches, not first clutches, as the tussocks flower after first clutches have already been laid.

Two-egg clutches are more susceptible than single clutches to early failure due to the additional effort required by the production and incubation of a second egg (Monaghan & Nager 1997). This explains the higher proportion of viable eggs in one-egg nests (84%, 79–87% CI) than in two-egg-nests (72%, 70–74% CI). Cold winters also have a negative effect on egg viability, with 5% less viable eggs for every degree Celsius difference in mean winter temperature, most likely because of the poor condition of the birds at the start of the breeding season. This is consistent with the results of a previous study on the viability of eggs transferred to captivity (Eason & Willans 2001).

Similar to the egg viability results, single clutches have higher hatching success (93%, 88–97% CI vs 84%, 77–91% CI) and fledging success (45%, 38–52% CI vs 38%, 28–46% CI) than two-egg clutches, which is again a likely consequence of the additional effort required for the production and incubation/provisioning of a second egg/chick (Heaney & Monaghan 1995, 1996; Monaghan et al. 1998). Hatching success in captivity (83%, 70–86% CI) is lower than in one-egg nests in the wild (93%, 88–97% CI), but is more than compensated for by the greater fledging success and survival over the first winter. For further discussion of the causes of egg failure in captivity, see Eason & Willans (2001). With hatching success lower in captivity than in the wild, one might conclude that it is best to transfer chicks rather than eggs. But eggs are removed mainly from two-egg nests, where the probability of both eggs hatching is only 77% (67–85% CI), and the hatching success of each egg is 84% (77–91% CI). The transfer of eggs to captivity thus has no negative impact on the hatching success of two-egg clutches. Also, when an egg rather than a chick is transferred from a single clutch, the lower hatching success in captivity is balanced by a higher probability of the pair re-nesting. This is because the probability of re-nesting is higher after nest failure in the egg stage (22%, 18–27% CI) than after failure in the chick stage (10%, 7–15% CI).

Our results provide some evidence that egg viability and the probability of re-nesting decrease with increasing population density. This would suggest that (up until the recent population crash in 2007/08) the amount of suitable breeding habitat in the Murchison Mountains was nearing carrying capacity. However, if the effect of winter temperature is removed from the models, the effect of population density on probability of re-nesting and on egg viability becomes non-significant. This is because of a positive correlation between winter temperature and population size over the study period.

The fact that several territories that were occupied in the past have been vacant in recent years is also an argument against the takahē population in the Murchison Mountains having approached carrying capacity. Overall, we need to treat these results with caution and cannot draw any firm conclusions in support or against population density effects on takahē in the Murchison Mountains.

If we combine clutch size, egg viability, hatching success and fledging success, the average number of chicks fledged in the wild from a single clutch is 0.35, while the number of chicks fledged from a double clutch is 0.39. In terms of overall reproductive output, it makes sense for takahē to lay two eggs. Fledging success of double clutches left with one egg (54%, 45–62% CI) is higher than for unmanaged single clutches (37%, 31–43% CI). This suggests that pairs that lay two eggs are fitter, and/or have settled in higher quality territories, and once they are relieved of the burden of double parenting, the chances of them successfully raising a chick improve substantially. Fledging success in captivity (87%, 79–91% CI) is substantially higher than in the wild. If we combine hatching success, fledging success and survival over the first winter, the probability of a viable egg producing a one-year-old bird is 65.0% in captivity vs 27.6% in the wild. This, combined with the observation that the adult survival rate of captive-reared birds is the same as for wild birds, suggests that the captive rearing programme makes a substantial positive contribution to the population dynamics of the takahē in the Murchison Mountains. Unless stoats can be effectively controlled or removed, we recommend that captive rearing remain an integral part of the takahē recovery programme.

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## References

- Ballance A 2001. Takahe: the bird that twice came back from the grave. In: Lee WG, Jamieson IG eds *The takahe: fifty years of conservation management and research*. Dunedin, University of Otago Press. Pp. 18–22.
- Barker RJ 1997. Joint modelling of live-recapture, tag-resight and tag-recovery data. *Biometrics* 53: 666–677.
- Basse B, Flux I, Innes J 2003. Recovery and maintenance of North Island kokako (*Callaeas cinerea wilsoni*) populations through pulsed pest control. *Biological Conservation* 109: 259–270.

- Bunin JS, Jamieson IG, Eason D 1997. Low reproductive success of the endangered Takahe *Porphyrio mantelli* on offshore island refuges in New Zealand. *Ibis* 139: 144–151.
- Cormack RM 1964. Estimates of survival from the sightings of marked animals. *Biometrika* 51: 429–438.
- Crouchley D 2001. Murchison Mountain stoat control – Project plan. Unpublished report, Department of Conservation, Te Anau, New Zealand.
- Eason DK, Willans M 2001. Captive rearing: a management tool for the recovery of endangered takahe. In: Lee WG, Jamieson IG eds *The takahe: fifty years of conservation management and research*. Dunedin, University of Otago Press. Pp. 80–95.
- Frederiksen M, Wanless S, Harris MP 2004. Estimating true age-dependence in survival when only adults can be observed: an example with Black-legged Kittiwakes. *Animal Biodiversity and Conservation* 27(1): 541–548.
- Gil-Delgado JA, Marco E, Paredes M, Vives-Ferrández C 2005. Seasonal clutch size variation of multi-brooded bird species: comparisons between breeding season and latitudes. *Ibis* 147: 206–212.
- Gray RD, Craig JL 1991. Theory really matters: hidden assumptions in the concept of ‘habitat requirements’. *Acta XX Congressus Internationalis Ornithologici* 4: 2553–2560.
- Greaves G, Joice N 2007. Takahe Programme Annual Report – 1 June 2006 to 31 May 2007. Unpublished report, Department of Conservation, Te Anau, New Zealand.
- Greaves G, Wickes C, Joice N 2008. Takahe Programme Annual Report – 1 June 2007 to 30 June 2008. Unpublished report, Department of Conservation, Te Anau, New Zealand.
- Grueber CE, Jamieson IG 2008. Quantifying and managing the loss of genetic variation in a free-ranging population of takahe through the use of pedigrees. *Conservation Genetics* 9: 645–651.
- Grueber CE, Laws RJ, Nakagawa S, Jamieson IG 2010. Inbreeding depression accumulation across life-history stages of the endangered Takahe. *Conservation Biology* 24: 1617–1625.
- Hamilton S 2005. Takahe demography report, Murchison Mountains. Unpublished report, Department of Conservation, Te Anau, New Zealand.
- Hamilton S, Maxwell JM, Greaves G 2006. Analysing the efficacy of nest manipulation techniques on the breeding success of takahe (*Porphyrio hochstetteri*), Murchison Mountains, Fiordland National Park. Unpublished report, Department of Conservation, Te Anau.
- Heaney V, Monaghan P 1995. A within-clutch trade-off between egg production and rearing in birds. *Proceedings of the Royal Society B* 261: 361–365.
- Heaney V, Monaghan P 1996. Optimal allocation of effort between reproductive phases: the trade-off between incubation costs and subsequent brood rearing capacity. *Proceedings of the Royal Society B* 263: 1719–1724.
- Hegg D 2006. Evaluating the effectiveness of the Murchison Mountains stoat trapping programme: A preliminary assessment, 2002–2005. *Wildlife Management Report* 196, Department of Zoology, University of Otago, Dunedin, New Zealand.
- Hegg D 2007. Use of a stochastic population model as a tool to assist decision making in the management of Takahe (*Porphyrio hochstetteri*). Unpublished MSc thesis, University of Otago, Dunedin, New Zealand. 207 p.
- Hitchmough R, Bull L, Cromarty P comps 2007. *New Zealand Threat Classification System lists – 2005*. Wellington, Department of Conservation. 194 p.
- IUCN 2006. 2006 IUCN Red List of Threatened Species™. Online at <http://www.iucnredlist.org> (accessed 1 June 2007).
- Jamieson IG, Ryan CJ 2001. Island takahe: Closure of the debate over the merits of introducing Fiordland takahe to predator-free islands. In: Lee WG, Jamieson IG eds *The takahe: fifty years of conservation management and research*. Dunedin, University of Otago Press. Pp. 96–113.
- Jamieson IG, Roy MS, Lettink M 2003. Sex-specific consequences of recent inbreeding in an ancestrally inbred population of New Zealand takahe. *Conservation Biology* 17: 708–716.
- Jolly GM 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. *Biometrika* 52: 225–247.
- King CM 1983. The relationships between beech (*Nothofagus* sp.) seedfall and populations of mice (*Mus musculus*), and the demographic and dietary responses of stoats (*Mustela erminea*), in three New Zealand forests. *Journal of Animal Ecology* 52: 141–166.
- Loman J 1982. A model of clutch size determination in birds. *Oecologia* 52: 253–257.
- Lunn DJ, Thomas A, Best N, Spiegelhalter D 2000. WinBUGS – A Bayesian modelling framework: Concepts, structure, and extensibility. *Statistics and Computing* 10: 325–337.
- Maxwell JM 2001. Fiordland takahe: population trends, dynamics and problems. In: Lee WG, Jamieson IG eds *The takahe: fifty years of conservation management and research*. Dunedin, University of Otago Press. Pp. 61–79.
- Maxwell JM 2010. Takahe minimum disturbance study. Murchison Mountains 1999–2007. Unpublished report, Department of Conservation, Te Anau, New Zealand.
- Maxwell JM, Christie JE 2005. Takahe egg and chick mortality field study. Unpublished report, Department of Conservation, Te Anau, New Zealand.
- Maxwell JM, Jamieson IG 1997. Survival and recruitment of captive-reared and wild-reared takahe in Fiordland, New Zealand. *Conservation Biology* 11: 683–691.
- McKone MJ, Kelly D, Harrison AL, Sullivan JJ, Cone AJ 2001. Biology of insects that feed in the inflorescences of *Chionochloa* (Poaceae) in New Zealand and their relevance to mast seeding. *New Zealand Journal of Zoology* 28: 89–101.
- McLennan JA, Potter MA, Robertson HA, Wake GC, Colbourne R, Dew L, Joyce L, McCann AJ, Miles J, Miller PJ, Reid J 1996. Role of predation in the decline of kiwi, *Apteryx* spp., in New Zealand. *New Zealand Journal of Ecology* 20: 27–35.
- Mills JA 1978. Population studies of takahe. In: *Seminar on the Takahe and its Habitat: proceedings: Te Anau, 5-6 May, 1978*. Invercargill, Fiordland National Park Board. Pp. 52–72.
- Mills JA 1990. Research involvement in the management of takahe: a case study. *Science & Research Internal Report* 64. Wellington, Department of Conservation. 6 p.
- Mills JA, Mark AF 1977. Food preferences of takahe in Fiordland National Park, New Zealand, and the effect of competition from introduced red deer. *Journal of Animal Ecology* 46: 939–958.

- Mills JA, Lavers RB, Lee WG, Garrick AS 1982. Management recommendations for the conservation of takahe. Unpublished report, N.Z. Wildlife Service (now Department of Conservation, New Zealand).
- Mills JA, Lee WG, Lavers RB 1989. Experimental investigations of the effects of takahe and deer grazing on *Chionochloa pallens* grassland, Fiordland, New Zealand. *Journal of Applied Ecology* 26: 397–417.
- Monaghan P, Nager RG 1997. Why don't birds lay more eggs? *Trends in Ecology & Evolution* 12: 270–274.
- Monaghan P, Nager RG, Houston DC 1998. The price of eggs: increased investment in egg production reduces the offspring rearing capacity of parents. *Proceedings of the Royal Society B* 265: 1731–1735.
- Ratcliffe N, Catry P, Hamer KC, Klomp NI, Furness RW 2002. The effect of age and year on the survival of breeding adult Great Skuas *Catharacta skua* in Shetland. *Ibis* 144: 384–392.
- Seber GAF 1965. A note on the multiple-recapture census. *Biometrika* 52: 249–259.
- Sheldon BC, Kruuk LEB, Merilä J 2003. Natural selection and inheritance of breeding time and clutch size in the collared flycatcher. *Evolution* 57: 406–420.
- Spiegelhalter DJ, Best NG, Carlin BP, Van der Linde A 2002. Bayesian measures of model complexity and fit. *Journal of the Royal Statistical Society B* 64: 583–639.
- Trewick SA 1996. Morphology and evolution of two takahe: flightless rails of New Zealand. *Journal of Zoology* 238: 221–237.
- Trewick SA, Worthy TH 2001. Origins and prehistoric ecology of takahe based on morphometric, molecular, and fossil data. In: Lee WG, Jamieson IG eds *The takahe: fifty years of conservation management and research*. Dunedin, University of Otago Press. Pp. 31–48.
- Wickes C, Crouchley D, Maxwell J 2009. Takahe (*Porphyrio hochstetteri*) recovery plan 2007–2012. *Threatened Species Recovery Plan* 61. Wellington, Department of Conservation. 56 p.

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**Appendix 1.** Tables of breeding-success model selection results

Takahē (*Porphyrio hochstetteri*) breeding success in the Murchison Mountains, Fiordland, New Zealand, 1981–2007. Model selection according to the DIC criterion.

Model equations for binomial events:

$$N_{Success,j} \sim \text{Binomial}(P_{Success,j}, N_j), \text{logit}(P_{Success,j}) = \beta_0 + \sum_i \beta_i \cdot \text{Factor}_i + \varepsilon(j)$$

Model equations for multinomial events:

$$N_{i,j} \sim \text{Multinomial}(P_{i,j}, N_{Trials,j}), \text{logit}(P_{i,j}) = \beta_{0,i} + \sum_k \beta_{k,i} \cdot \text{Factor}_k + \varepsilon(j)$$

**Table A1.** Probability of nesting (first nests only)

Model factors	Dbar	Dhat	pD	DIC	ΔDIC
1 LogBeech	114.1	94.3	19.8	134.0	
2 Constant	114.5	95.0	19.6	134.1	0.1
3 N Takahe	114.4	94.7	19.7	134.1	0.2
4 N_Takahe, Log(Beech)	114.1	94.1	20.0	134.2	0.2
5 Log(Beech), Snow	114.0	93.7	20.2	134.2	0.3
6 N_Takahe, Tussock, Log(Beech)	114.0	93.6	20.3	134.3	0.4
7 Tussock, Log(Beech), Snow	113.8	93.3	20.5	134.4	0.4
8 N_Takahe, Log(Beech), Snow	114.1	93.7	20.4	134.5	0.5
9 N_Takahe, Tussock	114.4	94.2	20.1	134.5	0.5
10 N_Takahe, Winter Temp, Tussock, Log(Beech), Summer Rain	113.6	92.7	20.9	134.5	0.6
11 N_Takahe, Tussock, Snow	114.1	93.7	20.4	134.6	0.6
12 N_Takahe, Tussock, Log(Beech), Snow	114.0	93.3	20.7	134.7	0.7
13 N_Takahe, Winter Temp, Tussock, Log(Beech), Snow	113.8	92.8	20.9	134.7	0.7
14 N_Takahe, Winter Temp, Tussock, Log(Beech), Summer Rain, Snow	113.6	92.3	21.3	134.9	0.9

**Table A2.** Probability of re-nesting

Model factors	Dbar	Dhat	pD	DIC	ΔDIC
1 Egg/Chick, N_Takahe, Tussock, Winter Temp, Snow	143.6	129.3	14.3	157.8	
2 Egg/Chick, N_Takahe, Tussock, Winter Temp	142.6	126.4	16.2	158.9	1.0
3 Egg/Chick, N_Takahe, Log(Beech), Tussock, Winter Temp, Snow	143.6	128.2	15.4	158.9	1.1
4 Egg/Chick, N_Takahe, Tussock, Winter Temp, Snow, Summer Rain	143.6	128.2	15.4	159.0	1.1
5 Egg/Chick, N_Takahe, Winter Temp, Snow	143.3	127.2	16.1	159.4	1.6
6 Egg/Chick, Tussock, Winter Temp, Snow	143.7	126.8	17.0	160.7	2.8
7 Egg/Chick, N_Takahe, Tussock, Snow	143.7	125.9	17.8	161.5	3.7
8 N_Takahe, Tussock, Winter Temp, Snow	159.3	147.5	11.9	171.2	13.3

**Table A3.** Size of first clutch

Model factors	Dbar	Dhat	pD	DIC	ΔDIC
1 Snow, Winter Temp	160.4	137.0	23.4	183.9	
2 Log(Beech), Winter Temp, Snow	159.4	134.3	25.1	184.5	0.7
3 N_Takahe, Winter Temp, Snow	160.4	136.1	24.3	184.7	0.8
4 Log(Beech), Snow	159.8	134.6	25.2	185.0	1.2
5 Winter Temp	161.5	137.9	23.6	185.1	1.3
6 N_Takahe, Log(Beech), Winter Temp, Snow	159.6	133.9	25.7	185.3	1.5
7 N_Takahe, Log(Beech), Winter Temp, Rain, Snow	160.3	135.3	25.0	185.4	1.5
8 Snow	161.5	137.5	24.0	185.4	1.6
9 N_Takahe, Log(Beech), Winter Temp, Rain	160.4	134.8	25.5	185.9	2.0
10 Constant	162.7	138.7	23.9	186.6	2.7
11 N_Takahe, Log(Beech), Snow	160.1	133.6	26.5	186.6	2.8
12 Log(Beech), Winter Temp	161.5	136.2	25.2	186.7	2.9
13 N_Takahe, Log(Beech), Winter Temp	161.7	136.0	25.7	187.4	3.6

Note: Best model parameters are of difficult biological interpretation. Cold winters and winters of high snowfall would have a positive effect on clutch size.

**Table A4.** Size of second clutch

Model factors	Dbar	Dhat	pD	DIC	ΔDIC
1 Tussock	84.6	72.4	12.2	96.8	
2 N_Takahe, Tussock, Winter Temp	82.6	68.0	14.6	97.2	0.4
3 N_Takahe, Tussock, Winter Temp, Rain	84.0	70.4	13.6	97.6	0.8
4 N_Takahe, Tussock, Winter Temp, Rain, Snow	82.9	68.1	14.8	97.6	0.8
5 N_Takahe, Tussock	83.4	69.2	14.2	97.7	0.9
6 N_Takahe, Log(Beech), Tussock, Winter Temp, Rain, Snow	82.4	66.9	15.5	97.8	1.0
7 Tussock, Winter Temp	84.2	70.3	13.9	98.1	1.3
8 Constant	81.9	65.6	16.3	98.3	1.5
9 N_Takahe, Winter Temp	80.2	61.3	18.9	99.1	2.3

**Table A5.** One-egg nest viability

Model factors	Dbar	Dhat	pD	DIC	ΔDIC
1 Constant	72.6	63.7	8.9	81.5	
2 N_Takahe	72.4	62.9	9.5	82.0	0.5
3 N_Takahe, Summer Rain	72.0	61.9	10.1	82.1	0.6
4 Winter Temp	72.6	63.0	9.6	82.2	0.7
5 Snow	72.7	62.9	9.8	82.5	1.1
6 Summer Rain	72.9	63.2	9.7	82.6	1.1
7 Winter Temp, Summer Rain	72.6	62.4	10.2	82.8	1.3
8 Winter Temp, Snow	72.7	62.2	10.4	83.1	1.6
9 N_Takahe, Winter Temp, Summer Rain	72.5	61.7	10.8	83.4	1.9
10 Summer Rain, Snow	73.2	62.6	10.6	83.8	2.3
11 Winter Temp, Snow, Summer Rain	73.0	61.8	11.2	84.1	2.6
12 N_Takahe, Log(Beech), Tussock, Winter Temp, Rain, Snow	73.3	60.1	13.2	86.6	5.1

**Table A6.** Two-egg nest viability

Model factors	Dbar	Dhat	pD	DIC	ΔDIC
1 N_Takahe, Winter Temp	180.0	159.5	20.5	200.6	
2 N_Takahe, Winter Temp, Summer Rain	179.1	157.3	21.8	200.8	0.3
3 Winter Temp	180.8	160.5	20.3	201.1	0.5
4 N_Takahe, Winter Temp, Snow	180.1	158.7	21.4	201.5	0.9
5 N_Takahe, Winter Temp, Snow, Summer Rain	178.9	156.0	22.9	201.8	1.2
6 Summer Rain, Winter Temp	181.3	159.8	21.5	202.8	2.2
7 Constant	183.6	163.9	19.7	203.3	2.8
8 N_Takahe, Log(Beech), Tussock, Winter Temp, Summer Rain, Snow	178.7	153.2	25.5	204.2	3.6
9 N_Takahe	183.8	163.3	20.5	204.2	3.7
10 Summer Rain	183.1	161.5	21.6	204.7	4.1
11 N_Takahe, Summer Rain	183.2	161.1	22.1	205.2	4.7

**Table A7.** Hatching success for one-egg nests

Model factors	Dbar	Dhat	pD	DIC	ΔDIC
1 Constant	164.9	151.7	13.2	178.1	
2 Summer Rain	166.1	153.3	12.8	178.8	0.7
3 Winter Temp, Summer Rain	166.0	152.0	14.0	180.0	1.9
4 N_Takahe, Winter Temp, Summer Rain, Log(Beech)	165.4	149.4	16.0	181.5	3.3
5 N_Takahe, Winter Temp, Summer Rain	165.8	150.7	15.1	181.0	2.8
6 Summer Rain, Tussock	166.4	153.7	12.7	179.0	0.9
7 N_Takahe, Summer Rain	165.9	151.8	14.0	179.9	1.8
8 N_Takahe, Summer Rain, Log(Beech)	165.3	150.4	15.0	180.3	2.2
9 Summer_Rain, Log(Beech)	166.2	152.5	13.6	179.8	1.7
10 Log(Beech)	164.6	150.3	14.3	178.8	0.7
11 Summer_Rain, Log(Beech), Tussock	166.3	152.6	13.7	179.9	1.8
12 Tussock	165.1	151.9	13.2	178.3	0.2
13 Summer_Rain, Log(Beech), Snow	165.7	150.8	15.0	180.7	2.6
14 Summer_Rain, Log(Beech), Snow, Tussock	165.3	149.3	16.0	181.3	3.1
15 Summer_Rain, Log(Beech), Snow, Tussock, Winter Temp	165.0	147.9	17.1	182.0	3.9
16 Summer_Rain, Log(Beech), Snow, Tussock, Winter Temp, N_Takahe	164.8	146.7	18.1	182.9	4.8
17 Summer_Rain, Log(Beech), Snow, N_Takahe	164.9	148.7	16.2	181.1	3.0

**Table A8.** Hatching success for two-egg nests

Model factors	Dbar	Dhat	pD	DIC	ΔDIC
1 Summer Rain	57.6	47.6	10.0	67.6	
2 Summer_Rain, Log(Beech), Snow	56.7	45.8	10.9	67.6	0.0
3 Summer_Rain, Log(Beech)	57.1	46.1	11.0	68.1	0.5
4 Constant	59.3	50.2	9.1	68.4	0.7
5 Snow	58.8	49.2	9.6	68.4	0.8
6 Winter Temp, Summer Rain	57.4	46.2	11.2	68.6	1.0
7 Summer_Rain, Log(Beech), Snow, Tussock	56.4	44.3	12.2	68.6	1.0
8 Summer_Rain, Snow	58.0	47.2	10.7	68.7	1.1
9 Summer Rain, Tussock	57.5	45.9	11.6	69.1	1.5
10 Summer_Rain, Log(Beech), Tussock	56.8	44.3	12.5	69.3	1.7
11 Summer_Rain, Log(Beech), Snow, N_Takahe	57.7	45.7	12.0	69.8	2.1
12 Log(Beech)	59.1	48.2	10.9	70.0	2.4
13 Tussock	59.6	48.7	10.9	70.4	2.8
14 N_Takahe, Summer Rain	58.8	46.7	12.1	70.9	3.3
15 N_Takahe, Summer Rain, Log(Beech)	58.4	45.8	12.6	71.0	3.3
16 N_Takahe, Winter Temp, Summer Rain	58.3	45.2	13.1	71.4	3.8
17 N_Takahe, Winter Temp, Summer Rain, Log(Beech)	58.1	44.8	13.4	71.5	3.9
18 Summer_Rain, Log(Beech), Snow, Tussock, Winter Temp, N_Takahe	57.8	43.5	14.3	72.2	4.6

**Table A9.** Fledging success for one-egg nests

Model factors	Dbar	Dhat	pD	DIC	ΔDIC
1 Constant	227.5	216.3	11.2	238.7	
2 Tussock	227.4	214.9	12.5	239.8	1.1
3 Snow	227.4	215.0	12.5	239.9	1.2
4 N_Takahe	228.0	216.0	12.0	240.0	1.3
5 Tussock, Snow	227.5	213.9	13.6	241.0	2.3
6 N_Takahe, Tussock	227.9	214.7	13.2	241.2	2.4
7 N_Takahe, Winter Temp	228.6	215.9	12.7	241.2	2.5
8 N_Takahe, Snow	228.0	214.8	13.2	241.3	2.5
9 Winter Temp, Snow	227.8	214.2	13.6	241.4	2.7
10 N_Takahe, Snow, Summer Rain	228.1	213.8	14.3	242.4	3.6
11 N_Takahe, Winter Temp, Snow	228.7	215.0	13.7	242.4	3.7
12 N_Takahe, Winter Temp, Log(Beech)	228.9	215.4	13.6	242.5	3.8
13 N_Takahe, Log(Beech), Snow	228.4	214.2	14.2	242.5	3.8
14 N_Takahe, Winter Temp, Log(Beech), Summer Rain	229.1	214.6	14.5	243.7	4.9
15 N_Takahe, Winter Temp, Summer Rain, Snow	229.0	214.3	14.7	243.7	5.0

**Table A10.** Fledging success for one-egg nests

Model factors	Dbar	Dhat	pD	DIC	ΔDIC
1 Constant	76.0	69.0	7.0	83.1	
2 Tussock, Snow	74.4	65.6	8.8	83.2	0.1
3 N_Takahe, Winter Temp	74.3	65.3	9.0	83.3	0.2
4 N_Takahe, Winter Temp, Tussock, Log(Beech), Snow	71.6	59.9	11.7	83.3	0.2
5 N_Takahe, Snow	74.5	65.4	9.1	83.5	0.5
6 N_Takahe, Winter Temp, Tussock, Log(Beech), Snow, Summer Rain	71.6	59.5	12.0	83.6	0.5
7 N_Takahe, Winter Temp, Log(Beech), Summer Rain	72.6	61.5	11.1	83.7	0.7
8 Winter Temp, Tussock, Log(Beech), Snow	72.7	61.3	11.4	84.1	1.1
9 N_Takahe, Snow, Summer Rain	74.5	64.8	9.7	84.2	1.2
10 N_Takahe, Log(Beech), Snow	74.6	64.9	9.7	84.3	1.3
11 Tussock	76.5	68.3	8.2	84.7	1.6
12 N_Takahe, Winter Temp, Tussock, Log(Beech), Summer Rain	72.8	60.9	11.9	84.7	1.7
13 N_Takahe	77.1	68.8	8.3	85.4	2.4
14 N_Takahe, Tussock	77.6	68.4	9.2	86.8	3.7

Note: Several models score a very similar DIC. However, when looking at the model parameters for tussock seeding, snowfall, population density, etc., it is seen that those effects are inconsistent, i.e. there is no monotonous relationship between the number of chicks fledged and the model parameters. A constant model should thus be chosen simply because of the difficulty of giving a biological explanation to any other model parameters.