

Using adaptive management to determine requirements of re-introduced populations: the case of the New Zealand hihi

DOUG P. ARMSTRONG,*† ISABEL CASTRO* and RICHARD GRIFFITHS‡

*Wildlife Ecology Group, Institute of Natural Resources, Massey University, Private Bag 11222, Palmerston North, New Zealand; †Oceania Chair, IUCN-SSC Re-introduction Specialist Group; and ‡Department of Conservation, Warkworth Area Office, PO Box 474, Warkworth, New Zealand

Summary

1. Adaptive management involves the development of predictive models, strategic manipulation of management actions to gain information, and subsequent updating of the models and management. The paradigm has several characteristics that make it an effective approach for determining requirements of re-introduced populations.

2. Adaptive management was applied to the re-introduction of hihi *Notiomystis cincta*, a New Zealand forest bird that had been reduced to a single island population. Following three previous failed re-introductions, we initiated an 8-year series of management manipulations when hihi were re-introduced to Mokoia Island in 1994.

3. We developed a population model for projecting outcomes under potential management scenarios, and updated it on an annual basis. The population model combined submodels for survival and reproduction that were selected from sets of candidate models using an information-theoretic approach. All projections incorporated demographic stochasticity, and later projections incorporated uncertainty associated with model selection and parameter estimation.

4. The programme showed that some actions (e.g. the provision of sugar water during breeding season and mite control) substantially increased the population's growth rate, but that persistence was uncertain under any management scenario. The population growth rate was shown to be constrained by a low adult survival rate that was unaffected by supplementary feeding, and was associated with a feature of the island (high density of *Aspergillus fumigatus* spores) that could not be remedied by management. Hihi were therefore removed from Mokoia. However, the management actions shown to be effective on Mokoia have now been used to produce sustained growth in three other re-introduced hihi populations.

6. *Synthesis and applications.* The results illustrate how adaptive management can facilitate successful species recovery. Without manipulation of management treatments, the Mokoia hihi re-introduction would have just been another failure that provided no useful information. Instead, our manipulations allowed us to identify effective management actions that were successfully applied to other re-introduced populations, and allowed us to identify a limiting factor that had not been previously considered. We have illustrated how other characteristics of the adaptive management approach (flexible treatments, ongoing monitoring, early model development, quantitative projections and incorporation of uncertainty) were essential to the programme.

Key-words: adaptive management, model selection, population modelling, population viability analysis, re-introduction, species recovery, uncertainty

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Introduction

The process of adaptive management involves developing explicit models of how systems work, manipulating management of those systems to gain information, then updating models to guide subsequent management (Holling 1978; Walters 1986). The adaptive management approach emphasizes ongoing monitoring, recognition of uncertainty, flexibility in management options, and involvement of stakeholders in model development and management decisions. The flexibility in management distinguishes the approach from classic experimentation, where replicated treatments and controls are planned in advance (Lee 1999). However, adaptive management should not be confused with trial-and-error approaches, where no explicit models are developed.

The adaptive approach is potentially applicable to a wide range of problems in conservation biology. However, while the concept of adaptive management is widely advocated, there are few examples of true adaptive management of wildlife populations (Williams, Nichols & Conroy 2002; Sutherland 2006). Related to this, Pullin *et al.* (2004) and Sutherland (2006) suggested that the majority of decisions in practical conservation management are not based on scientific evidence, and Fazey, Fischer & Lindenmayer (2005) showed that only a small proportion of the papers published in conservation biology journals assess the effectiveness of conservation actions. There appears to be a considerable gap between conservation research and conservation practice, and the adaptive management approach provides a potential means of bridging this gap.

An area of conservation practice that can clearly benefit from the adaptive management approach is re-introduction of threatened species. Re-introductions are a popular option for conservation managers, partially because they show evidence of action being taken to recover threatened species or restore ecosystems. However, historically, species re-introductions have had a poor success rate, and it has long been recognized that research is required to improve this situation (IUCN 1987; Scott & Carpenter 1987; Griffith *et al.* 1989). There has been a recent explosion in the number of publications on re-introduction, yet the majority of these simply document case studies without explicitly developing models or testing hypotheses (Seddon, Armstrong & Maloney 2007).

Adaptive management can be applied to several types of decisions involved in re-introduction programmes. Varley & Boyce (2006) used adaptive management for predicting the impact of a predator re-introduction on prey populations, and Dimond & Armstrong (2007) used adaptive management for predicting numbers of animal that could be removed from a source population. Hirzel *et al.* (2004) noted that post-release movements of mobile animals could be used to improve habitat suitability models, meaning

criteria for release sites could be updated adaptively. Surprisingly, however, a recent literature search by Seddon, Armstrong & Maloney (2007) found that no published studies had used adaptive management to determine the conditions required for a re-introduced population to persist. If post-release management can be varied over time or between individuals in a population, strategic manipulation of management treatments can be used to gain information needed for predictive models. These models can be used not only to guide ongoing management of the population, but also to predict site suitability and management requirements for future re-introductions. This mode of inference should be more efficient than *post hoc* comparative analyses of re-introductions (Griffith *et al.* 1989; Wolf, Garland & Griffith 1998), given that multiple re-introductions are not required and it is subject to far fewer confounding factors.

Predictions about population persistence are subject to considerable uncertainty (Fieberg & Ellner 2000; Ellner *et al.* 2002), particularly with small populations. Managers need to take this uncertainty into account when deciding whether the benefits of a management action justify its costs, and whether to invest in further monitoring and experimentation. Predictions made through adaptive population management should therefore take the form of distributions of outcomes, where these distributions account for uncertainty associated with parameter estimates, model structure and demographic stochasticity (White 2000a; Wade 2002).

We applied adaptive management to a re-introduced population of an endangered New Zealand bird, the hihi *Notiomystis cincta* (Du Bus). Following failed re-introductions of this species to three islands, we initiated an 8-year adaptive management programme when hihi were re-introduced to a fourth island, Mokoia, in 1994. We conducted a series of manipulations designed to assess the effects of supplementary feeding and mite control on vital rates, and we developed a population model to predict persistence under different management regimes. The population model combined submodels for survival and reproduction that were selected from sets of candidate models using an information-theoretic approach (Burnham & Anderson 2002). The model was updated on an annual basis, and subsequent management decided at annual hihi recovery group meetings involving wildlife managers, scientists, field workers and Iwi (tribal) representatives. The programme revealed management actions that were effective and ineffective for increasing vital rates, but also revealed that there was a substantial risk of decline because of a low adult survival rate under all management regimes. This low survival appeared to be because of aspects of the island's habitat that could not be addressed by management and, hence, the birds were removed to another island in 2002. However, the effective management actions identified have now been used to produce sustained growth in two other re-introduced hihi populations. We outline the management and monitoring

procedures followed over the 8 years, then illustrate the modelling performed on the final data set and present the distributions of outcomes obtained from that model. Finally, we illustrate how key aspects of the adaptive management approach were essential for obtaining the information necessary to make the management decisions.

Data and methods

SPECIES AND STUDY SITE

Hihi are cavity-nesting forest birds that feed on a variety of fruit and nectar sources as well as invertebrates (Higgins, Peter & Steele 2001). Typically they breed from October to March, and can raise up to two broods per season, with up to 5 young per brood. They usually breed in pairs, but their mating system is characterized by frequent extra-pair copulations (Castro *et al.* 1996) and males can fertilize several females (Ewen, Armstrong & Lambert 1999; Castro *et al.* 2004). Males do not contribute to nest building and incubation, and usually make only a minor contribution to provisioning of chicks (Castro *et al.* 1996; Ewen & Armstrong 2000; Low, Joy & Makan 2006).

Hihi were originally found throughout the North Island of New Zealand as well as on several offshore islands, but by the late 19th century they survived only on Hauturu (3800 ha), which is the least modified of New Zealand's forested islands. The decline of hihi is attributed to forest clearance and introduction of exotic mammalian predators, with pathogens possibly playing a role (Taylor, Castro & Griffiths 2005). Attempts to establish hihi on three predator-free islands in the 1980s were unsuccessful. It was hypothesized

that the regenerating forest on these islands provided insufficient nectar and fruit (Lovegrove 1985; Castro 1995), leading to our experimental food supplementation programme when hihi were subsequently re-introduced to Mokoia. Forty hihi (20 males and 20 females) from Hauturu were released on Mokoia in September 1994.

Mokoia (38°05'S, 176°17'E) is a 135-ha volcanic island in Lake Rotorua on the North Island of New Zealand. It was largely cleared for cultivation hundreds of years ago, then designated a Wildlife Refuge in the 1950s and left to regenerate. Closed-canopy broadleaf forest had developed over part of the island by 1994, but regeneration had been slowed by feral livestock and Norway rats *Rattus norvegicus* (Berkenhout) until these exotics were eradicated in 1989–90. The forest remained highly modified in comparison with Hauturu, with a much lower canopy, a dominance of seral tree species and a complete absence of large tree cavities (Perrott & Armstrong 2000).

MANAGEMENT PROCEDURES

We manipulated the availability, distribution and quality of supplementary food (Table 1). The food provided was either 20% sugar water solution or a solution of honeyeater and lorikeet mix (Wombaroo Food Products, Glen Osmond, SA, Australia) with the same sugar concentration. The latter provided protein and other nutrients as well as sugar, and was used only during the breeding season. Food was presented in commercial hummingbird feeders (Perky-Pet Products Co, Denver, CO, USA no. 212-P), which were used readily by hihi. We provided food continuously for the first 4 months to facilitate establishment of the population, and started manipulations in January 1995.

Table 1. Summary of adaptive management of the re-introduced hihi population on Mokoia Island. The programme combined management manipulations with population modelling to identify effective management actions and assess population persistence under possible management regimes. Years are divided into non-breeding (March–October) and breeding (October–March) periods. We provided supplementary food [either sugar water (E, energy) or Wombaroo® honeyeater and lorikeet mix (E + P, energy plus protein)] at some times but not others, and altered the distribution of supplementary food (one to four communal feeders or individual feeders placed at some or all nest sites)

Year(s)	Supplementation regime		Outcomes	Adaptations
	Non-breeding	Breeding		
1995–96, 1996–97, 1997–98	E* (communal)	E + P (some nests)	On-off feeding (1995) suggests no effect on survival. Distance to feeder has no effect on no. fledglings. Population projected to decline if mites not controlled, uncertain otherwise	Try removing winter supplementation. Try removing breeding-season supplementation. Early control of mites in all nests
1998–99	–	–	Fledglings female ⁻¹ much lower than previously. Population projected to decline rapidly if not fed during breeding season, uncertain otherwise	Provide feeders during breeding season. Try reducing cost by switching to communal sugar water feeders in breeding season
1999–2000	–	E (communal)	Juvenile survival may be lower without feeding. Fledglings female ⁻¹ similar to 1995–96 to 1997–98. Population projections uncertain re. growth or decline	Communal feeder(s) throughout year. Continue streamlined management. Continue monitoring
2000–01, 2001–02	E (communal)	E (communal)	Population projected to grow under management, but substantial risk remains (Figs 2–4)	Department of Conservation decides to relocate remaining hihi to Kapiti Island

*Food available continuously except for January–October 1995 when available (16 days) and unavailable (12 days) on on–off regime.

We manipulated food availability on both a short-term and long-term basis. In 1995, we conducted an 'on-off' supplementation experiment, in which sugar water was available (for 16 days) then unavailable (for 12 days) on an alternating basis for 10 months (Armstrong & Perrott 2000). In subsequent years food was provided continuously or was completely absent throughout each breeding period (October–March) or non-breeding period (March–October).

We manipulated food distribution during the breeding season by providing feeders to individual females or by providing communal feeders. Females nesting on one side of the island were given feeders (10 m from nest site) in 1995–96, and females on the opposite side were given individual feeders in 1996–97 (for a map of nest locations and the two sides see Castro *et al.* 2003). The other females needed to fly 190–810 m to access the nearest feeder in these years. All females were given individual feeders in 1997–98, no feeders were provided in 1998–99, and three to four communal feeders were provided in subsequent years. We manipulated the quality of food provided during the breeding season by switching from Wombaroo® (1995–96 to 1997–98) to sugar water in later years.

We provided wooden nest boxes to compensate for the absence of tree cavities, and these were used readily by hihi. Sufficient boxes were provided so that nest sites were not a limiting resource.

We initiated mite control during the first breeding season after discovering that blood-sucking nest mites *Ornithonyssus bursa* could build up to levels where they killed hihi broods (Armstrong *et al.* 1999). Initially we left each nest alone until mites built up to near lethal levels, then intervened by shifting the brood to a hand-built nest in a clean nest box (Taylor & Castro 2000). This protocol allowed us to estimate the proportion of broods that would have been lost without mite control, and therefore the extra productivity gained through management.

REPRODUCTION ANALYSIS

We recorded the number of young fledged by each female each year. The final data set had 70 observations (70 female-years) collected over seven breeding seasons, with 46 individual females occurring one to four times in the data set. We excluded the first season's data given that the females' ages were unknown and birds were translocated shortly before the breeding season.

We used various procedures for analysing reproduction, assessing the effects of female age (*a*), supplementary energy (*e*), supplementary protein (*p*) and distance from nest site to nearest feeder (*d*) on the number of fledglings per female per year (*f*). The first three factors were dichotomous (age divided into first-year and older), whereas distance was usually treated as a covariate. Ultimately, we used Proc GENMOD and Proc NLMIXED in SAS® (SAS Institute 2003), treating the number of fledglings per female per year as a Poisson-distributed random variable with a log-link function.

Use of Proc NLMIXED allowed us to fit models where year or individual female was treated as a random factor, thereby enabling us to assess whether changes in productivity associated with supplementary feeding could be accounted for by random yearly variation, and whether the apparent effect of any fixed factor could be a confound of variation among females.

SURVIVAL ANALYSIS

We surveyed the island for hihi to obtain mark-resighting data used to estimate survival (all hihi were colour-banded prior to translocation and subsequently as nestlings). Initially we conducted fortnightly surveys (Armstrong & Perrott 2000), then biannual surveys in October (pre-breeding) and March (post-breeding). The final analysis used 15 biannual surveys conducted from March 1995 to March 2002 (the first 6 months after translocation were excluded) and encounter histories for 184 birds.

We modelled survival using the live-recaptures option in program MARK (White & Burnham 1999). The analysis recognized two age classes, adults and juveniles, with birds becoming adults at the start of the breeding season after hatching. Sexes of many juveniles were unknown, so juveniles needed to be excluded when fitting sex-specific adult survival models. Therefore we performed separate analyses for adult and juvenile survival. For both analyses, we initially modelled factors affecting resighting probability, then used the best resighting model when comparing survival models.

For the juvenile survival analysis, birds were considered to be 'captured' at the post-breeding survey after they fledged, then 'recaptured' when encountered in subsequent surveys. Birds were considered to become adults after one interval (at a pre-breeding survey) and were then assumed to have a constant adult survival probability. We always took juvenile survival probability to be time dependent in the global model, and considered two simpler models where juvenile survival was affected by energy supplementation (*e*) or was constant (.).

For adult survival analysis, birds were divided into two groups (males and females). Birds were considered to be 'captured' when first encountered as an adult, then 'recaptured' when encountered in subsequent surveys. We always used the fully time-dependent survival model (ϕ_{gxt}) as the global model, and considered a set of simpler candidate models where adult survival was affected by sex (*g*), season (*s*) and/or energy supplementation (*e*) or was constant.

POPULATION MODELLING

Discrete-time population models were used to project population growth under different management scenarios. These population models combined estimates of vital rates (survival and reproduction) derived from the analyses described above. A female-only approach

was used for simplicity, given that males make little parental investment, can potentially fertilize multiple females and were never likely to be substantially outnumbered by females. We never included density dependence, as the population was at low density throughout our study and our population projections were for short time frames.

Initially we used the package VORTEX (Lacy 2000) but later constructed population models in Microsoft® Excel spreadsheets. Benefits of the spreadsheet approach included flexibility, transparency and ability to share models with the wide range of people familiar with Excel spreadsheets. The spreadsheet models included both deterministic models, which were used to obtain probability distributions for λ (finite rate of increase) under different management regimes, and stochastic models, which were used to obtain distributions of outcomes that took demographic stochasticity into account.

We calculated λ from the Leslie matrix:

$$\begin{bmatrix} 0.5s_j s_b f_1 & 0.5s_j s_b f_{2+} \\ s_a & s_a \end{bmatrix}$$

where f_1 is the mean number of fledglings per first-year female with mite control, f_{2+} is the mean number of fledglings per older female with mite control, s_b is the probability that a female's broods will not be killed by mites, s_j is the probability that a fledgling will survive to the breeding season, 0.5 is the probability that a surviving fledgling will be female (this assumption was supported by the data), and s_a is the probability that an adult female will survive 1 year. λ is the dominant eigenvalue of the matrix, so was obtained using the EigVal function from the PopTools (Hood 2005) add-in to Excel.

To account for uncertainty in parameter estimates and model structure (White 2000a), we obtained multiple values for λ where each vital rate was sampled from a distribution defined by its estimate and standard error. Reproductive rates (f) were assumed to be log-normally distributed and survival rates (s) to be logit-normally distributed. We used the delta method (Cox 1998) to calculate approximate standard errors for each vital rate under each model, and used model averaging (Buckland, Burnham & Augustin 1997) to obtain overall estimates and standard errors that accounted for ambiguity in model selection. Models were excluded from the averaging process if they had AIC weights < 0.01. Calculations were performed in Excel, with random values obtained using the NORMINV and RAND() functions.

We added demographic stochasticity to spreadsheet models using Excel functions (White 2000b). The number of young fledged was obtained using the PopTools function dPoissonDev (mean), where mean is the expected number of fledglings. The numbers of adult and juvenile females surviving to the start of each breeding season were obtained using the Excel function CRITBINOM (trials, probability_s, alpha), where

trials is the maximum number, probability_s is the estimated survival probability, and alpha is selected using the RAND() function. For juveniles, the survival probability was multiplied by 0.5 to simulate random sex allocation.

Results

ADAPTIVE MANAGEMENT

The number of breeding females fluctuated from 11 to 16 over the first few breeding seasons (Fig. 1), and our initial results suggested that supplementary feeding had no effect on vital rates (Table 1). The on-off supplementation experiment in 1995 showed that hihi did not lose condition, or have lower survival, when supplementary food was removed (Armstrong & Perrott 2000). The experiment during the 1996–96 and 1996–97 breeding seasons showed that even though females greater than 50 m from feeders used them only rarely (Castro *et al.* 2003), distance to feeders had no effect on productivity. In contrast, tracking of mite infestations up to the 1996–97 breeding season suggested that females would have lost their broods in seven of 24 cases (29%) if there had been no intervention. Population projections were ambiguous regarding whether growth would occur with mite control, but suggested a decline was likely without control.

We therefore treated all nests to prevent mite build-up after the 1996–97 breeding season. We also decided

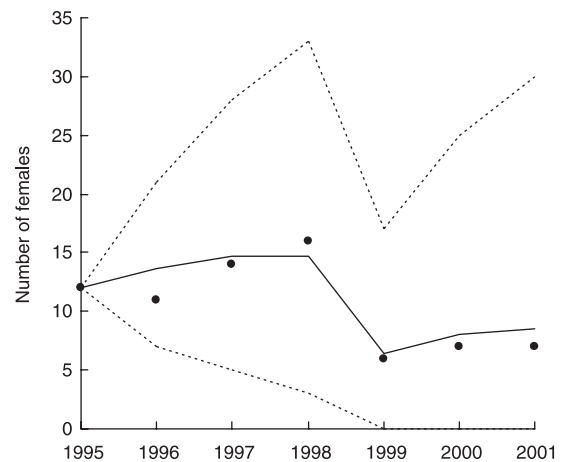


Fig. 1. Observed changes in number of female hihi on Mokoia Island (at the start of breeding season) in comparison with retrospective projections from the final population model. The dots show observed numbers of females, the solid line shows the mean numbers of females from 10 000 runs of the model, and the dotted lines show the 2.5% and 97.5% percentiles. Simulations started with six first-year females and six older females, matching the observed numbers at the start of the 1995–96 breeding season. The expected values for vital rates varied across years following changes in supplementary feeding regime (Table 1). The values for each run were selected from distributions defined by the estimates and standard errors for the vital rates (Table 4), and the simulations included demographic stochasticity in survival, reproduction and sex allocation.

at this stage to collect a further year of data with supplementary feeding, with all females given individual feeders during the breeding season, then to try relaxing management by not providing supplementary food (Table 1).

Productivity was negligible (0.33 fledglings female⁻¹) in 1998–99, when no supplementary food was available, in comparison with the previous three breeding seasons (mean 3.3 fledglings female⁻¹). The number of breeding females consequently dropped from 16 to six between 1998–99 and 1999–00 (Fig. 1). Analysis of juvenile survival up to 1999 also suggested a tentative drop in juvenile survival when supplementary food was unavailable. Projections based on these data were still ambiguous under supplementary feeding and mite control, but suggested a rapid drop to extinction without breeding season supplementation.

Following these results, supplementary food was provided continuously after September 2000. However, we tried streamlining the breeding season supplementation by providing three to four communal feeders (based on the result that close access to feeders was unnecessary) and by providing sugar water rather than Wombaroo® (Table 1). Data were collected under this management protocol until April 2002.

FINAL MODEL

The best reproduction model for the final data set was $\{a + e\}$ (Table 2), meaning the number of fledglings produced depended on the age of the female as well as whether supplementary energy was provided (first-year females fledged 40% fewer young on average than older females). Models that excluded either of these factors had negligible support ($w_i < 0.01$), including

Table 2. Models fitted to reproductive data to assess the effect of food supplementation regime on numbers of fledglings produced by hihi on Mokoia Island. The mean number of fledglings per female was modelled as a Poisson random variable with log-link function, and models were fitted using Proc NLMIXED in SAS. Models are listed from best to worst based on Akaike's information criterion, and models with negligible support ($w_i < 0.01$) are excluded. The overdispersion parameter \hat{c} ($\chi^2/\text{d.f.}$) was estimated to be between 1.26 and 1.31 for all models shown, indicating reasonable fits to the data

Model*	<i>K</i>	AIC _c	Δ_i	w_i
$a + e$	3	261.26	0.00	0.47
$a + e + p$	4	262.57	1.31	0.24
$a + e + d$	4	263.14	1.88	0.18
$a + e + p + d$	5	264.58	3.32	0.09

*Factors included in model: *a*, age of female (first year or older); *e*, energy supplementation (yes or no); *p*, complete food supplement (yes or no); *d*, distance to nearest feeder from female's nest site; *K*, number of parameters in model; AIC_c, Akaike's information criterion; Δ_i , difference in AIC_c value from that of the best model; w_i , Akaike weight.

models that allowed for random yearly variation. Adding individual female as a random factor had a negligible effect on model rankings, so we used simpler models that excluded this random factor. Four models had some support (Table 2) so were included in model averaging. All of these models had \hat{c} estimates between 1.26 and 1.31, showing reasonable fits to the data. The tentative support for the models $\{a + e + p\}$, $\{a + e + d\}$, $\{a + e + p + d\}$ could be interpreted to mean that protein supplementation and distance to feeders may have had some effect on reproduction. However, their support was largely because of having just one to two parameters more than the best model. Under the averaged model (Table 1), females were estimated to produce 5% more fledglings if given a complete food supplement rather than sugar water, and were estimated to produce 1% more fledglings if 10 m from a feeder rather than 175 m from a feeder (the mean distance with three to four communal feeders).

The best model for adult survival was $\{g\}$, meaning survival differed between sexes (40% lower in females) but was relatively constant over time. Ten different models were involved in model averaging (Table 3), including models incorporating an effect of supplementary food, but the inclusion of these models was solely because they only had one to two additional parameters. Under the averaged model, the annual survival of adult females was estimated to be 0.35 when supplementary food was available and 0.38 when it was unavailable. The juvenile survival models $\{e\}$ and $\{\}$ had similar levels of support (Table 3), meaning it was ambiguous whether supplementary feeding had any effect on juvenile survival, and there was negligible support for the fully time-dependent model. Under the averaged model, juvenile survival was estimated to be 0.45 with feeding and 0.38 with no feeding.

The global survival models fitted the data well, with \hat{c} estimated to be 1.12 for the juvenile analysis and 1.03 for the adult analysis. Resighting probability was estimated to be 0.95 (SE 0.025) for pre-breeding surveys and 0.67 (SE 0.056) for post-breeding surveys.

FINAL POPULATION PROJECTIONS

The parameter estimates used in our final population projections are summarized in Table 4. Retrospective projections from 1995 to 2002 gave a good fit to the observed trends in population size (Fig. 1) and age structure, giving a validation of the population model.

For projections into the future, it remained unclear whether the Mokoia hihi population would be likely to increase or decrease under further intensive management, although it was clear that the population would decline to extinction if no supplementary food was provided, and would almost certainly decline if mites were not controlled (Fig. 2). With a complete food supplement and nest mite control during the breeding season, and sugar water during the non-breeding season, λ was estimated to be 1.06, with 95% confidence limits

Table 3. Models fitted to bi-annual survey data to assess the effect of energy supplementation on survival of juvenile and adult hihi on Mokoia Island. Models were fitted using the live recaptures option in program MARK with a logit-link function. All models included two parameters for resighting probability (for pre- and post-breeding surveys), and the juvenile models included one parameter for adult survival. Models are listed from best to worst based on Akaike's information criterion, and models with negligible support ($w_i < 0.01$) are excluded. The overdispersion parameter \hat{c} was estimated to be 1.12 and 1.03 for the global models for juveniles and adult survival, respectively, indicating good fits to the data

Model*	K	AIC _c	Δ_i	w_i
Juveniles				
<i>e</i>	5	640.57	0	0.555
\cdot	4	641.05	0.48	0.436
Adults				
<i>g</i>	4	415.50	0	0.36
<i>g</i> + <i>s</i>	5	416.92	1.42	0.18
<i>g</i> + <i>e</i>	5	417.09	1.59	0.16
<i>g</i> × <i>s</i>	6	418.61	3.11	0.08
<i>g</i> + <i>s</i> + <i>e</i>	6	418.61	3.12	0.08
<i>g</i> × <i>e</i>	6	419.20	3.7	0.06
<i>s</i> × <i>e</i>	6	419.47	3.97	0.05
\cdot	3	420.85	5.35	0.02
<i>s</i>	4	422.30	6.80	0.01
<i>e</i>	4	422.53	7.03	0.01

*Factors included in survival model: *e*, energy supplementation (yes or no); *g*, sex (male or female); *s*, season (breeding or non-breeding); *K*, number of parameters in model; AIC_c, Akaike's information criterion corrected for small sample size bias; Δ_i , difference in AIC_c value from that of the best model; w_i , Akaike weight.

ranging from 0.83 to 1.29 (Fig. 2). With sugar water provided during the breeding season rather than the complete food supplement, λ was estimated to be 1.02, with 95% confidence limits ranging from 0.80 to 1.25.

Table 4. Estimates and standard errors for vital rates* used in final population projections for the Mokoia Island hihi under alternative management regimes (MC, mite control; E, energy supplementation; EI, energy supplementation in individual feeders†; E + P, energy and protein supplementation). The parameter s_b was estimated from our judgement that seven of 24 females would have lost their broods in the first three breeding season without intervention to control mites. Other estimates are weighted averages from models shown in Tables 2 and 3, and the standard errors shown account for uncertainty in model selection as well as parameter estimation

Rate	Management regime				
	MC	E	E, MC	EI, MC	E + P, MC
f_1	0.20 (0.10)	2.39 (0.31)	2.39 (0.31)	2.42 (0.33)	2.52 (0.35)
f_{2+}	0.33 (0.16)	3.97 (0.53)	3.97 (0.53)	4.01 (0.55)	4.19 (0.59)
s_b	1	0.71 (0.09)	1	1	1
s_j	0.38 (0.08)	0.46 (0.04)	0.46 (0.04)	0.46 (0.04)	0.46 (0.04)
s_a	0.38 (0.08)	0.35 (0.06)	0.35 (0.06)	0.35 (0.06)	0.35 (0.06)

* f_1 , mean number of young fledged per first-year female if mites controlled; f_{2+} , mean number of young fledged per older female if mites controlled; s_b , probability that a female's broods will not be killed by mites; s_j , probability that a fledgling will survive to the next breeding season; s_a , annual survival probability of adult females.

†Assumes feeder 10 m from breeding female rather than 175 m, the mean distance when three to four communal feeders provided.

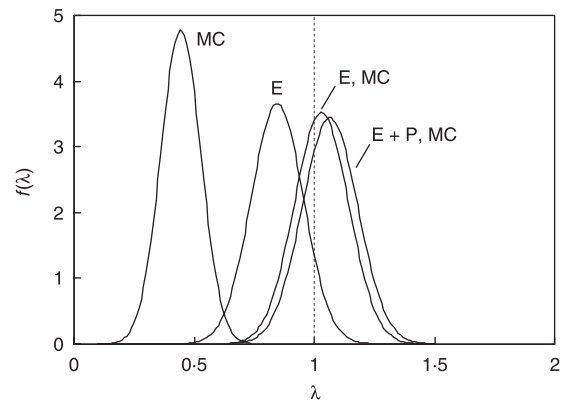


Fig. 2. Probability density functions for the expected growth rate (λ) of the Mokoia Island hihi population under different management regimes (E + P, supplementary energy and protein; E, supplementary energy; MC, mite control). λ -values were obtained from 10 000 sets of vital rates randomly selected from distributions defined by their estimates and standard errors (Table 4). Projections with supplementary feeding assume each female was 175 m from the nearest nest, but this distance had negligible effect on estimated reproductive rates (Table 4).

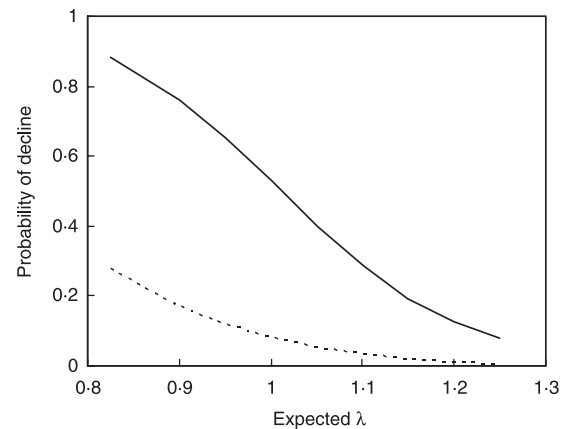


Fig. 3. Contribution of demographic stochasticity to the risk of population decline in Mokoia Island hihi. Curves show probabilities of decline (solid line) or extinction (broken line) over the 5 years from 2002 to 2007 as a function of the expected λ . Probabilities were estimated using a simulation model that included demographic stochasticity in survival, reproduction and sex allocation. The model was run 10 000 times at each λ -value, with λ varied by changing all vital rates by the same proportion. The initial population consisted of seven females (four first-year, three older), the number expected for the 2002–03 breeding season.

Projections incorporating demographic stochasticity showed that the fate of the population would be extremely uncertain even if λ was expected to be > 1 (Fig. 3). For these projections, we assumed that the breeding population in 2002–03 would consist of seven females (four first-year, three older), as this was the most likely scenario at the time of the final analysis. If expected vital rates were set at their point estimates for an intensive management scenario, so that λ was expected to be 1.06, it was estimated that there would be a 38% chance

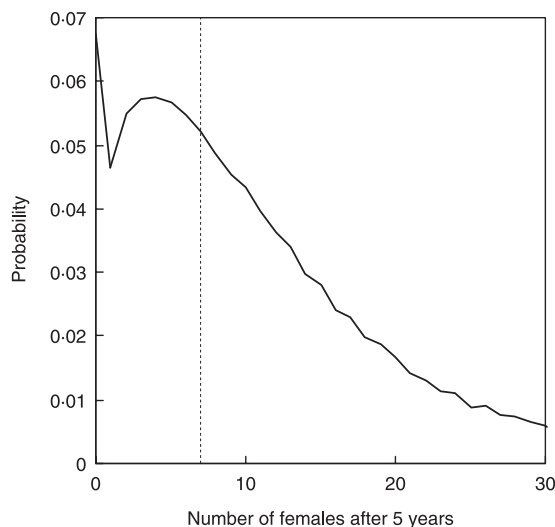


Fig. 4. Distribution of final projections for the Mokoia Island hihi population, accounting for uncertainty associated with parameter estimation, model structure and demographic stochasticity. Projections assumed intensive management (complete food supplement and mite control) for the 5 years from 2002 to 2007, starting with seven females. The distribution was based on 100 000 runs of a simulation model where vital rates were sampled from distributions at the start of each run (Table 4) and the subsequent trajectory affected by demographic stochasticity. The shape of the left-hand portion of the curve results from the fact that populations stay at zero once they reach this number.

that the population would decline over the next 5 years, and the most likely outcome was a decline to five to six females. When uncertainty in parameter estimation and model structure was added to the stochastic model, there was a 40% chance that the population would decline over 5 years, and the most likely outcome was a decline to three to four females (Fig. 4).

When presented with these projections, the New Zealand Department of Conservation decided not to invest further in managing the Mokoia hihi population. The remaining 12 birds were relocated to Kapiti Island to supplement another re-introduced hihi population that appeared to be growing in response to supplementary feeding.

Discussion

The Mokoia hihi programme illustrates seven key aspects of adaptive management that are highly applicable to re-introduced populations. First, probing the system through management manipulations (Walters 1986) enabled us to identify aspects of management that were effective for increasing vital rates, and aspects that had little or no effect. In particular, the data showed that reproductive success could be substantially improved by providing supplementary food during the breeding season, but that management could be relaxed by switching from Wombaroo® to sugar water (requiring less frequent cleaning) and by

providing communal feeders (easily accessed by boat) rather than individual feeders. The study therefore shows how an adaptive approach can be used not only to identify effective management actions but to streamline management to avoid unnecessary costs.

Second, early model development facilitated decision-making among stakeholders, as noted by both Holling (1978) and Walters (1986). Projections presented at annual recovery group meetings allowed participants to assess the effectiveness of management and, in particular, to appreciate the need for further data. Potentially, models can be constructed based on prior information before data collection begins, then updated using Bayes' theorem (Goodman 2002; Williams, Nichols & Conroy 2002), but in our case no data were available to obtain informative priors.

Third, quantitative predictions (Walters 1986) were essential for management decisions. It is sometimes suggested that population viability analyses should focus on qualitative comparisons of viability under different management options rather than quantitative predictions (Beissinger & Westfall 1998; McCarthy, Andelman & Possingham 2003). However, qualitative comparisons are insufficient to decide whether management is sufficient (Brook *et al.* 2002). Quantitative predictions for Mokoia hihi showed that the prescribed management treatments (supplementary feeding and mite control) were necessary for the population to persist but that a high risk of decline would remain under that management.

Fourth, flexible management (Holling & Meffe 1996) allowed us to expand our focus to issues that had not originally been considered. Our original hypothesis (Castro 1995) was that Mokoia hihi would be limited by poor survival because of insufficient fruit and nectar, and our initial experiment (Armstrong & Perrott 2000) targeted that hypothesis. However, subsequent manipulation of the food supplementation regime showed that it was reproduction rather than adult survival that responded to food supplementation.

Fifth, ongoing monitoring (Holling & Meffe 1996) led to the discovery that nest mites could kill hihi broods, and also led to the probable explanation for poor adult survival. Hihi corpses found during monitoring were subjected to post-mortem analysis, and most were found to have died from aspergillosis caused by the fungus *Aspergillus fumigatus* (Alley, Castro & Hunter 1999). As *A. fumigatus* is an opportunistic pathogen found mainly in soil, and birds are infected by exposure to spores, Perrott (2001) hypothesized that the poor survival of adult hihi on Mokoia was the result of high densities of *A. fumigatus* spores in the soil. Comparison of soil samples from Mokoia with similar samples from Tiritiri Matangi (where the re-introduced population has grown) and Hauturu (where hihi have always persisted) corroborated this hypothesis (Perrott 2001). It is not feasible to reduce *A. fumigatus* spore densities other than by simply allowing the forest to mature, nor is it feasible to treat aspergillosis in wild

bird populations. This evidence therefore reinforced the decision to remove the remaining hihi.

Sixth, flexible sequences of treatments rather than rigid experimental protocols (Lee 1999) allowed us to minimize risks to the population. We initially manipulated access of individual females to supplementary food through placement of feeders, and monitored feeder use and reproductive success. Distant females visited feeders rarely but did not have fewer fledglings, suggesting that production of fledglings was unaffected by feeders. Only at this stage did we completely remove the feeders, obtaining the result that reproduction was substantially reduced (re-analysis of feeder visitation data suggested that access to feeders was important during egg laying and chick rearing; Castro *et al.* 2003). Similarly, food limitation on survival was assessed initially through short-term manipulations designed to detect weight loss without risking starvation (Armstrong & Perrott 2000), and only when no weight loss was detected did we conduct longer term manipulations. Although our approach to mite control could not be described as adaptive management, this approach was designed to estimate the effect of management without leaving birds to die.

Finally, quantification of uncertainty (Walters 1986) was essential for informed management decisions. When deciding whether to invest in further management of the Mokoia hihi population, it was not the fact that the estimated λ was close to 1 that was so important but the fact that there was substantial uncertainty about the future population trajectory. Although it has been routine for some time to account for demographic stochasticity in population viability analyses, it is also essential that uncertainty associated with model selection and parameter estimation is accounted for (White 2000a; Wade 2002).

Although the hihi population was ultimately removed from Mokoia Island, the adaptive management programme has made an invaluable contribution to the hihi re-introduction programme. Without manipulation of management treatments, the Mokoia hihi re-introduction would have been just another failure that provided no useful information. Instead, our manipulations allowed us to identify effective management actions that were successfully applied to other re-introduced populations, and allowed us to identify a limiting factor that had not been previously considered. Application of the management protocol developed on Mokoia (sugar water supplementation at communal feeders and nest mite control) has now produced sustained growth in three other re-introduced hihi populations, on Kapiti and Tiritiri Matangi islands and at Karori Sanctuary. Consequently, the survival of the species no longer depends on the single remnant population on Hauturu.

We believe that the adaptive management approach we have illustrated could also be used to improve the success of many other re-introduction programmes. Although the management requirements of re-

introduced populations are clear in some cases, it is often more appropriate to treat management policies as hypotheses to be tested. With small populations of vulnerable species, it is inevitable that flexible sequences of management treatments will be needed rather than conventional experiments, and the data sets obtained will therefore lend themselves to information-theoretic model selection rather than traditional hypothesis testing (Burnham & Anderson 2002). It needs to be demonstrated that a re-introduced population has a positive finite rate of increase ($\lambda > 1$) under the prescribed management, given that initial populations are usually well below carrying capacity. Finally, it will be essential to account for uncertainty in most projections for re-introduced populations, given that small populations are prone to demographic stochasticity and that small sample sizes inevitably create uncertainty in both model selection and parameter estimation.

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