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Density-dependent population growth in a reintroduced population of North Island saddlebacks

DOUG P. ARMSTRONG*†, R. SCOTT DAVIDSON*, JOHN K. PERROTT*, JON ROYGARD* and LEN BUCHANAN‡

**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 ‡159 Waitaha Road, Welcome Bay, Tauranga, New Zealand*

Summary

1. Reintroductions provide a good opportunity to study density-dependent population growth, as populations can be studied at a range of densities and the change in density is not confounded with environmental conditions. An understanding of density dependence is also necessary to predict dynamics of reintroduced populations under different management regimens, and assess the extent to which they can be harvested for further reintroductions.

2. We monitored a North Island saddleback (*Philesturnus rufusater*) population for 6 years after reintroduction to Mokoia, a 135 ha island in New Zealand that was made suitable for saddlebacks by eradicating introduced Norway rats (*Rattus norvegicus*). We modelled adult and juvenile survival using Program MARK, and modelled numbers of young fledged per pair using Proc Mixed in SAS with individual female as a random factor.

3. Juvenile survival clearly declined as the population increased, and the decline was closely correlated with the number of breeding pairs. Reproduction also showed a clear decline that was explained by two factors: a difference in quality between territories occupied immediately after reintroduction and those occupied later, and an overall decline as the number of pairs increased. Reproduction was also strongly affected by age, and this needed to be accounted for when modelling density dependence.

4. A stochastic simulation model incorporating these dynamics closely predicted the observed population growth. The equilibrium population size was insensitive to density dependence in reproduction, but highly sensitive to density dependence in juvenile survival.

5. The model is being used to plan management strategies for potential reintroductions of saddlebacks to mainland areas with predator control. The species is currently confined to predator-free islands and one fenced mainland sanctuary.

Key-words: density-dependence, population dynamics, population modelling, program MARK, reintroduction.

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Introduction

Density dependence is a critical issue for our understanding and management of animal populations. There has been a long debate about the role of density dependence in population dynamics (Turchin 1995, 1999; Murray 1999), and this largely reflects the fact that density dependence is difficult to study. There is evidence for density dependence in a wide range of species (see Sinclair 1989 and Newton 1998 for reviews), but most studies can be challenged on statistical grounds (Wolda & Dennis 1993; den Boer & Reddingius 1996; Fox & Ridsdill-Smith 1996; Elkinton 2000; McCallum 2000).

Successive estimates of population density are not independent, so correlating population growth with density from such estimates can be misleading. Randomization methods have been developed to address

Correspondence: Doug P. Armstrong, Ecology Building 624, Massey University, Private Bag 11222, Palmerston North, New Zealand. E-mail: D.P.Armstrong@massey.ac.nz

this problem, but require 20–30 generations to detect density dependence (Shenk *et al*. 1998). It is less problematic to test for density dependence in vital rates (i.e. survival and reproduction). However, obtaining data on vital rates usually requires intensive fieldwork, and researchers must ensure that the measurement errors for vital rates and density are independent (Elkinton 2000). Furthermore, the factors causing changes in density may also affect species' environments, confounding the effect of density on subsequent population growth.

Experimental manipulation is the ideal solution to these problems because it can produce large changes in density that are not confounded with other factors. However, opportunities to perform such experiments are rare (e.g. Krebs *et al*. 1995), and experiments on too small a spatial scale may produce misleading results (e.g. Gould, Elkinton & Wallner 1990). Some of the best evidence for density dependence comes from game, where harvesting can be manipulated experimentally over a large scale and there is an economic incentive to obtain accurate data on vital rates (e.g. White & Bartman 1998).

Reintroductions also provide the opportunity to study density dependence, and such research is vital for many reintroduced populations. Animals are usually reintroduced at a low density, providing the opportunity to study how vital rates change as populations grow (Nicoll, Jones & Morris 2003), and this growth is unrelated to environmental change. The conservation value of reintroduced populations means that there is an incentive to estimate vital rates and understand how they change with density, as this information is needed to assess population viability. Where reintroductions are successful, they can provide the best source populations for future reintroductions so may be 'harvested' for this purpose. Such harvesting provides another manipulation of density (Dimond 2001), and provides an incentive to study density dependence to develop sensible harvest strategies.

These considerations are particularly relevant in New Zealand, where there have been numerous reintroductions to offshore or inland islands, often following eradication of introduced mammalian predators (Saunders 1994; Armstrong 1999–2005). Many of these island populations become source populations for further reintroductions, and some have been harvested repeatedly. Species are now starting to be reintroduced to mainland (North and South Islands) areas where predators are controlled. This means that harvesting of island populations will increase, and some could become permanent source populations for mainland 'sinks' if management does not allow positive growth.

In this paper we assess density dependence in an island population of North Island saddlebacks (*Philesturnus rufusater* Lesson) using data collected for 6 years after reintroduction. We compare alternative models for adult survival, juvenile survival and reproduction, some of which include density dependence and some of which do not. We estimate parameters under the best models, and combine these into a stochastic simulation model that can be used to guide future management of both island and mainland populations.

Methods

SPECIES AND STUDY AREA

The North Island saddleback is a medium-sized forest passerine belonging to the endemic Callaeatidae family. The North Island saddleback and South Island saddleback (*P. carunculatus* Gmelin) were considered the same species until recently, but were separated by Holdaway, Worthy & Tennyson (2001). Saddlebacks are primarily insectivorous but also eat nectar and fruit. They are territorial and sedentary, rarely leaving their territories once established. They become sexually mature in their first year, and form pairs that usually last until one member dies. They nest in tree cavities and other protected sites, and have a long breeding season. They nested from October–May in our study, rearing up to three broods of two to three young.

Saddlebacks are highly vulnerable to mammalian predators, and were extirpated from the mainland by the late 19th century (Lovegrove 1992). North Island saddlebacks survived on a single offshore island, but have been translocated to 13 additional islands since the early 1960s, establishing at least nine populations (Lovegrove 1996; Armstrong 1999–2005). They were released in a mainland area surrounded by a predator-proof fence in 2002, and were released in the first unfenced mainland area in 2004.

We studied the population on Mokoia, a 135-ha inland island in Lake Rotorua (38°05′ S; 176°17′ E) where 36 birds were released in April 1992 (Armstrong & Craig 1995). Mokoia is 2·1 km from the mainland at the nearest point, and this is much further than saddlebacks have been observed to fly (Merton 1975). Mokoia was formerly cleared for cultivation, but has now largely regenerated to forest (Perrott & Armstrong 2000). Norway rats (*Rattus norvegicus* Berkenhout) were eradicated from Mokoia in 1989–90, making it possible to reintroduce saddlebacks. The location of Mokoia means that it is the most convenient source population for most potential mainland reintroductions.

MONITORING

We surveyed the population from April 1992 to November 1997 to obtain data on population size, survival, reproduction and sex ratio of recruits. Each survey took 3 days, and involved walking a system of tracks and gullies that took us within 150 m of any point on the island. Saddlebacks call frequently, particularly when people walk nearby, and can be heard for well over 150 m. We investigated all saddlebacks heard, luring them with a tape-recorded call to attract them if necessary (both sexes respond to this), and recorded their identities and locations. We surveyed fortnightly during the breeding season and every 6–12 weeks at other times.

A subset of 24 surveys was used for estimating survival and population size from resightings of colour-banded birds. We banded 245 nestlings over the five breeding seasons in addition to the 36 originals, giving 281 birds in the data set. The surveys used were usually from March, June, September and December each year, giving four seasons. One additional survey was included, from early November 1996. This was 6 weeks after an aerial poison drop (an attempt to eradicate mice), and saddlebacks had abnormally high mortality over this period, due presumably to poisoning (Davidson & Armstrong 2002). Adding this survey meant we had two intervals for September–December 1996, and could exclude the effect of the post-poison interval when modelling survival.

Surveys during the breeding season were used to determine the number of young fledged by individual breeding pairs. We monitored all pairs found in the first 3 years, and a sample of 30–35 pairs in the last 2 years. We provided wooden nestboxes to facilitate monitoring, as natural nests usually take hours to locate. There did not appear to be a shortage of natural nest sites, and we did not expect the boxes to affect reproductive success. We nevertheless ensured that each pair had at least two boxes available so pairs did not differ in access to nestboxes. We recorded the contents of each box during surveys, and banded chicks 10–21 days after hatching (they fledge at about 28 days). Young were counted as fledged if observed in the nest at least 14 days after hatching, and checks of selected boxes suggested that there was no mortality from 14 days to fledging.

To detect young from natural nests, all pairs found during surveys were followed for up to 20 min if their current nesting status was unknown. Young may leave their parents after about 6 weeks, so we excluded pairs from the data set if we failed to observe them for 6 weeks and did not find their nest. Some fledglings die before their parents are observed, so counts of fledglings can underestimate the number fledged. We therefore also followed pairs that had used nestboxes, and used these observations to estimate fledgling survival (proportion surviving until their parents were observed) and detection probability.

ANALYSIS

Survival. We analysed survival using the 'live recaptures' option in MARK (White & Burnham 1999; http://www.cnr.colostate.edu/~gwhite/mark/mark.htm). We conducted separate analyses for adults and juveniles, with birds considered juveniles for 9 months after fledging. We used this age structure because (1) it was clear that juveniles had lower survival, (2) saddlebacks breed in their first year, starting at about 9 months of age, (3) alternative cut-off points gave a weaker fit to the data (Davidson 1999) and (4) analysis of the adult data divided into cohorts showed no evidence of further age structure. We conducted the analyses separately because it was important to distinguish between sexes (determined from behaviour and wattle size) when estimating adult survival, but this was not possible for juveniles. Potential sex differences in juvenile survival were accounted for by analysing the sex ratio of recruits (see below).

In the first analysis, birds were considered to enter the population when first encountered as adults and were excluded if never encountered as adults. In the second analysis, birds were considered to enter the population on the survey closest to their fledging date. This meant there were early and late fledgers each year, as some were recorded as first encountered in the December survey and others in the March survey. Birds remained in the data set after they became adults, but were then given separate adult parameters so they had no effect on model selection for juveniles. Population density was a covariate in both analyses, and was the estimated number of females at the start of the breeding season (we used the September survey each year except 1996, when the November survey was used due to mortality caused by the poison drop). We removed the effect of the poison drop from survival estimates by including a separate parameter for the post-poison interval in all models.

For adults, we initially assessed the fit of the model $\{\phi_{g*t}, P_{g*t}\}$ using program RELEASE. This model estimates survival (ϕ) and resighting (P) probabilities separately for each time interval (t) for both sexes (g). We also assessed whether the resighting model could be reduced to $\{P_t\}$, but did not attempt to reduce this model further as resighting rates were clearly variable. After confirming we had a suitable global model, we compared 15 simpler models in which survival was determined by different combinations of sex, season (s), year (y) and/or density (d). For juveniles, we initially assessed the fit of the global model $\{\phi_{f*t}, P_t\}$, where f refers to early and late fledgers. After confirming it had a good fit, we compared 13 simpler models in which juvenile survival probability was determined by different combinations of season, year, density and fledging date.

We also used MARK to estimate fledgling survival and detection probabilities, which were used to adjust the number of fledglings per pair when modelling reproduction. For this analysis, the encounter history for each fledgling sampled consisted of two recapture occasions, the first indicating whether it was seen with its parents (giving fledgling survival and detection probability) and the second indicating whether it was seen later. We considered four models, where fledgling survival and detection probability varied between years $\{\phi_y, P_y\}$, were constant $\{\phi., P.\}$, or one varied and the other was constant.

Population size. We estimated the number of females and the total population at each September survey (start of breeding), and in 1996 obtained a second estimate for the survey after the poison drop. Numbers of adults and juveniles were estimated separately since adults had higher resighting probabilities. The number in each age class was estimated as $n_t/\hat{P}_t$, where n_t and $\hat{P}_t$ are the number of individuals seen and estimated resighting probability for survey t. The standard error was estimated as $n_t[\mathrm{SE}(\hat{P}_t)]/(\hat{P}_t)^2$ (Wood *et al*. 1998). The model $\{\phi_t, P_t\}$ was used for both adults and juveniles, giving unconstrained estimates of resighting probability. Note that n_t includes unbanded birds, so the method assumes that unbanded birds were counted accurately and have the same detection probability as banded birds. The first assumption is reasonable because the birds held fixed territories by the start of breeding, and unbanded birds made up a minority of the population for most of the study so were unlikely to be confused with one another. The second assumption is reasonable because birds were sighted rather than captured, and there is no reason to expect banding in the nest to affect detection probability many months later.

Reproduction. We used Proc Mixed in SAS to analyse reproduction, using the adjusted number of fledglings per pair per year as the dependent variable. To avoid potential confounding due to pseudoreplication (Hurlbert 1984), we included the individual female as a random factor in all models. We used $\mathrm{AIC_c}$ to compare candidate models created using different combinations of independent variables.

We initially assessed how the effect of age should be modelled. We knew that first-year pairs bred later and produced fewer young, but did not know whether this was due to the age of the female, the age of the male, and/or lack of familiarity between them. We therefore considered models that included the age of the female (a_f; first-year or 1+), the age of the male (a_m; first-year or 1+), the ages of both birds ($a_f + a_m$), or the combined age of the pair (a_p; number of 1+ birds as a quantitative variable), and considered models that did or did not include the number of years the pair had been together (also a quantitative variable).

After finding the best age model, we considered models that did or did not include year (y), density (d), territory quality (t_2 or t_3), or region of the island. All were treated as class variables, except for density which is quantitative. We considered density to be the number of females in September, and did not use the post-poison estimate for 1996 as breeding locations, and probably resource availability, were determined by density before the poison drop. We modelled territory quality by designating locations as primary (those occupied in the year of the reintroduction), secondary (occupied in the second year) or tertiary (occupied later). This allowed an alternative form of density dependence, where productivity declines at high density due to most birds being forced into poor-quality territories, but remains similar on any territory. We considered models where all three classes were distinguished (t_3) or where secondary and tertiary territories were combined (t_2).

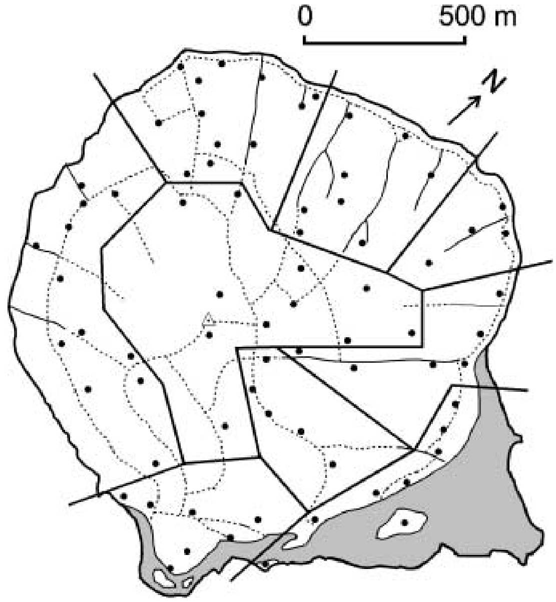

Fig. 1. Mokoia Island, showing the network of tracks (broken lines) and gulleys (solid lines) followed during surveys, and the nine regions into which the island was divided for the reproduction analysis (separated by bold straight lines). The black dots show the distribution of known saddleback pairs at the start of the 1996/97 breeding season. The island is covered by forest and regenerating scrub, except for the flat portion on the east side (shaded), which is mainly covered by grass and blackberry.

We divided the island into nine regions based on vegetation, topography and distribution of pairs (Fig. 1). The different combinations of these variables considered gave 22 candidate models.

Sex ratio of recruits. We counted the number of males and females in each cohort known to survive for at least 9 months after fledging, and compared three models for explaining the data: (1) expected sex ratio 50 : 50, (2) expected sex ratio constant but not 50 : 50 and (3) sex ratio changes with density. We fitted the third model using logistic regression in SAS, with the same measure of density as for survival analysis. We calculated the likelihood of each model by hand based on probability theory and converted these to $\mathrm{AIC_c}$.

Population model. We constructed a stochastic matrix model for the population using a spreadsheet in Microsoft Excel (White 2000). The spreadsheet tracked the number of males and females in the population at the start of each breeding season, distinguishing between first-year and older birds. It converted these into numbers of pairs of different age classes, assuming that that older birds would be preferred as mates and that unpaired birds of either sex would not reproduce. It calculated the expected number of fledglings (α) for that year based on the best reproduction model. It then used the formula ROUND(GAMMAINV(RAND(),α,1),0) to obtain the actual number, meaning the program picked a random number from a Poisson distribution with mean α (the Gamma distribution with $\beta = 1$ is a continuous analogue to the Poisson). It then obtained the number of female fledglings using the formula CRITBINOM(trials,probability,RAND()), meaning the number was sampled from the binomial distribution where 'trials' is the number of fledglings and 'probability' is the chance of being female. The spreadsheet calculated the probability of each fledgling and adult surviving to the next breeding season that year based on the best models for juvenile and adult survival. Finally, it determined the actual number of adults and fledglings surviving to the next breeding season using CRITBINOM(trials,probability,RAND()), where 'trials' was the maximum number and 'probability' was adult or juvenile survival probabilility.

We ran the 'Calculate' function 1000 times using a macro, and obtained the 2·5% and 97·5% percentile for the number of females at the start of each year. We then altered the spreadsheet to assess sensitivity of the output to different forms of density dependence.

Results

POPULATION SIZE

The estimated population in September 1992 was 35 birds, with 33 known to be alive, so there was little mortality from the 36 birds released in April 1992. The population grew over the next 4 years, reaching about 217 in September 1996, dropped following the poison drop at the end of that month, then recovered to about 200 in September 1997 (Fig. 2). The population was always male-biased, the estimated number of females being 40–46% of the total population. All females observed during the breeding season were paired, so the estimated number of females equals the number of breeding pairs.

SURVIVAL

We used $\{\phi_{g*t}, P_t\}$ as the global model for adult survival as it had a good fit to the data ($P = 0{\cdot}820$ for TEST 2 + TEST 3 in RELEASE). It had a much lower AIC_c than $\{\phi_{g*t}, P_{g*t}\}$, meaning there was no indication that resighting probabilities differed for males and females. Comparison of adult survival models showed $\{\phi.\}$ and $\{\phi_d\}$ to explain the data best (Table 1). These two models had similar support, meaning it is unclear whether adult survival was constant or declined with density. Annual adult survival probability declined over time (Fig. 3), but the decline from 1995/96 to 1996/97 is not predicted by $\{\phi_d\}$ because density was lower in 1996/97 (estimated in November) than in 1995/96. Models $\{\phi_g\}$ and $\{\phi_{g+d}\}$ also had $\Delta AIC_c < 2$ (Table 1), but this is because distinguishing between sexes adds only one parameter. Estimated annual survival probabilities were extremely close for males (0·88) and females (0·90). Models incorporating variation among seasons or random variation among years had negligible support.

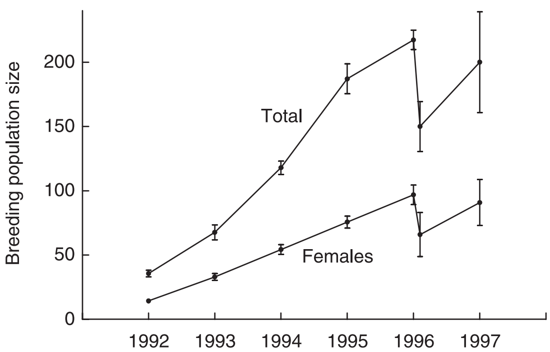

Fig. 2. Growth of the Mokoia Island saddleback population following reintroduction of 36 birds (16 female, 20 male) in April 1992. Points show the estimated number of birds (top) and females (bottom) at the start of each breeding season (September). Vertical bars show standard errors. An aerial drop of brodifacoum cereal pellets was conducted in September 1996, resulting in the decline in population from September to November that year.

Table 1. Comparison of models for factors affecting adult survival. The factors considered in survival models (ϕ) were population density (d), sex (g), season (s) and year (y), with interactions (*) or without interactions (+). Models were selected based on Akaike's information criterion (AIC_c), the lowest AIC_c indicating the most parsimonious model. K is the number of parameters in the model, ΔAIC_c is the difference in AIC_c between the current model and the best model, and w_i is the Akaike weight (the relative support for the model). Sixteen survival models were considered, and those with negligible support ($\Delta AIC_c > 6$) are not listed. The resighting model was $\{P_t\}$ in all cases, meaning resighting probability was estimated for each survey

Model	K	ΔAIC_c	w_i
$\phi.$	26	0·00	0·30
ϕ_d	27	0·04	0·29
ϕ_g	27	1·53	0·14
ϕ_{g+d}	28	1·60	0·13
ϕ_{g*d}	29	3·33	0·06
ϕ_{s+d}	30	4·92	0·03

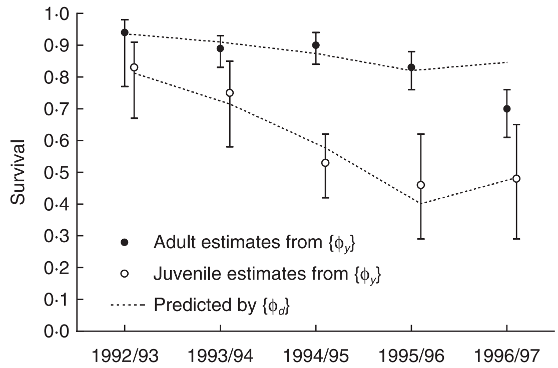

Fig. 3. Survival of adult and juvenile saddlebacks in the 5 years after reintroduction to Mokoia Island. Points show the estimated probability of an adult surviving 12 months or a juvenile surviving for 9 months after fledging. Vertical bars show 95% confidence intervals. The interval from September–November 1996 is discounted in the analysis, eliminating the effect of the poison operation on the 1995/96 estimate. Dotted lines show predictions of models where survival probability declines with density (Table 1, Table 2).

Table 2. Comparison of models for factors affecting juvenile survival. Factors considered were population density (d), fledge date (f), season (s) and year (y). Other conventions as in Table 1. Fourteen survival models were considered, and those with negligible support ($\Delta AIC_c > 6$) are not listed. Resighting probability for juveniles was modelled as $\{P_t\}$ in all cases, and survival and resighting probabilities for adults (birds > 9 months old) were modelled as $\{\phi., P_t\}$ (see Table 1)

Model	K	ΔAIC_c	w_i
ϕ_d	50	0·00	0·41
ϕ_{f+d}	51	1·69	0·18
ϕ_{s+d}	53	2·07	0·15
ϕ_{s+y}	56	2·23	0·13
ϕ_{f*d}	52	2·94	0·09

Estimated resighting probabilities ranged from 0·35 to 0·91, with a mean of 0·67.

The global model $\{\phi_{f*t}, P_t\}$ for juvenile survival, combined with the model $\{\phi., P_t\}$ once birds reached adulthood, also had a good fit to the data (observed deviance lower than mean from bootstrap test). The best model for juvenile survival was clearly $\{\phi_d\}$ (Table 2), giving strong evidence of density dependence, and this model closely predicts the decline over time (Fig. 3). The only other model with $\Delta AIC_c < 2$ was $\{\phi_{f+d}\}$, and this is due to it having only one additional parameter (overall survival probabilities were 0·63 and 0·64 for early and late fledgers, respectively). Estimated resighting probabilities for juveniles ranged from 0·12 to 1·00, with a mean of 0·49.

REPRODUCTION

We measured reproduction of 13 pairs in 1992/1993, 26 in 1993/1994, 48 in 1994/1995, 31 in 1995/1996 and 26 in 1996/1997. There were 241 fledglings from known nest sites, and 113 fledglings from unknown sites were observed with their parents. We obtained fledgling survival data for 178 of the birds from known sites, and estimated fledging survival and detection probability to be 0·87 and 1·00, respectively, based on $\{\phi., P.\}$, which was clearly the best model. We therefore divided brood sizes from unknown sites by 0·87, resulting in 17·6 fledglings being added. The adjusted number of fledglings per female per year ranged from 0 to 7·3, with a mean of 2·6. General linear models (Table 3) had a good fit to these data in terms of normality and homoscedasticity, so no transformation was required.

Age effects on reproduction were best explained by the variable a_p, the number of age 1 + birds in the pair. Taking age into account, the reproductive rate clearly declined as the population grew (Fig. 4). The best model for explaining the data was $\{a_p + t_2 + d\}$, meaning that pairs on primary territories (those occupied in the first year) produced more fledglings than other pairs, but productivity on all territories declined with density (Table 3). This model closely predicted the decline in reproduction (Fig. 4). The model $\{a_p + t_2 * d\}$ had a ΔAIC_c of 1·4, potentially suggesting an interaction between territory quality and density, but this is due largely to the model having only one additional parameter. The model $\{a_p + t_2\}$ had some support ($\Delta AIC_c = 2{\cdot}3$), suggesting that the overall effect of density is ambiguous, but this model failed to predict the decline in productivity in years 4–5 (Fig. 4). The model $\{a_p + d\}$, which ignores territory quality, received negligible support and poorly predicted the shape of the decline in productivity (Fig. 4). There was negligible support for any model that did not take territory quality into account, or for models that separated the island into regions.

Table 3. Comparison of models for factors affecting numbers of fledglings per breeding pair per year. Factors considered were the number of age 1 + birds in the pair (a_p), territory quality (t_2, t_3), population density (d), year (y) and region of the island (see Fig. 1). With t_2, there was a distinction between territories occupied in the first year after reintroduction and those occupied later. With t_3, there was a further distinction between territories occupied in the second year and those occupied later. Other conventions as for Table 1. Models were fitted to the data using Proc Mixed in SAS, with the individual female included as a random factor in all models. Twenty-two models were considered, and those with negligible support ($\Delta AIC_c > 6$) are not listed

Model	K	ΔAIC_c	w_i
$a_p + t_2 + d$	6	0	0·46
$a_p + t_2 * d$	7	1·4	0·23
$a_p + t_2$	5	2·3	0·14
$a_p + t_2 + y$	9	4·5	0·05
$a_p + t_3 + d$	6	4·8	0·04
$a_p + t_3 * d$	7	6·0	0·02

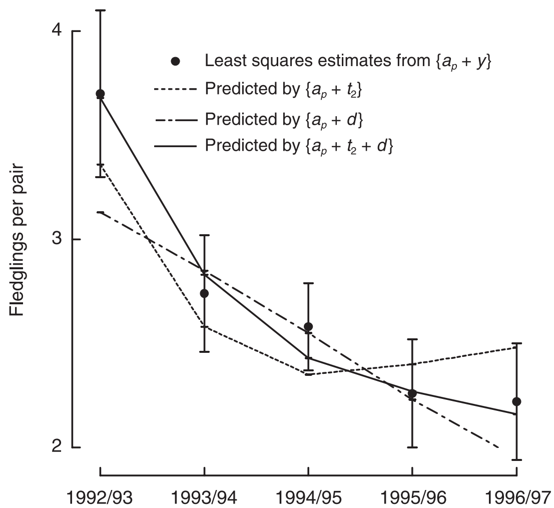

Fig. 4. Decline in reproduction of saddlebacks in the 5 years after reintroduction to Mokoia Island. Points show least squares means (± SE) from the model $\{a_p + y\}$ (Table 3), which corrects for changes in age distribution, and lines show predictions of alternative density-dependent models. Model $\{a_p + t_2\}$ distinguishes between territories occupied in the first year after reintroduction and those occupied later, model $\{a_p + d\}$ includes a linear decline with density, and model $\{a_p + t_2 + d\}$ includes both factors (Table 4).

SEX RATIO

Of the 111 recruits observed from 1993 to 1997, 49 (44%) were female. This accounts for the male-biased sex ratio in the breeding population throughout the study. However, the model assuming a 50 : 50 expected ratio ($K = 1$) was the most parsimonious explanation for the data, suggesting the skew could have occurred by chance. The model where a constant sex ratio was estimated from the data ($K = 2$) had some support ($\Delta AIC_c = 0{\cdot}54$, $w_i = 0{\cdot}37$), but there was no evidence for density dependence in sex ratio ($K = 3$; $\Delta AIC_c = 2{\cdot}52$).

POPULATION MODEL

We constructed the population model using models selected for survival and reproduction (Table 4), and with each recruit having a 50% chance of being female. We initially used the best models for density dependence, meaning adult survival was constant, juvenile survival declined with density and reproduction was higher for primary than secondary territories and also declined with density (Table 4). We assumed that the 14 primary territories would be occupied by older pairs, as was usually the case, and included the constraint that the mean fledglings/female for any age class could not fall below zero. The mean growth curve from the simulations closely approximated the observed growth (Fig. 5a), and the average population size reached an equilibrium of 118 females after 9 years.

We then assessed the effects of adding or removing different forms of density dependence. Adding density dependence to adult survival gave a similar curve, but with a more accurate prediction of population size after the poison drop (Fig. 5b). This model predicted an average of 98 females at equilibrium. Changing the reproduction model had little effect, the average equilibrium population being 119–121 females when alternative forms of density dependence were used (Fig. 5c,d), and 123 females when density dependence in reproduction was removed altogether (Fig. 5e). In contrast, removing density dependence in juvenile survival completely changed the dynamics (Fig. 5f), giving an equilibrium population of 339 females that was not reached for about 15 years.

Discussion

Our results provide strong evidence of density dependence in reproduction and juvenile survival, and tentative evidence of density dependence in adult survival. The data used to estimate reproduction and juvenile survival were separate from those used to estimate population density, so these analyses do not suffer from the lack of independence inherent in many attempts to detect density dependence (den Boer & Reddingius 1996; Elkinton 2000; McCallum 2000). The reproduction data were obtained by a different procedure (monitoring individual pairs), and the surveys used to estimate juvenile survival were conducted after those used to estimate density and involved a different set of birds. There is some overlap in the data used to estimate adult survival and population density, so the tentative relationship between these variables could be criticized on these grounds. However, the survival estimates are based on four surveys per year, the resighting probabilities are high and we observed the population at a wide range of densities relative to the estimation error. Hoyle's (1993) analysis of the reintroduced population on Tiritiri Matangi Island also suggested density dependence in reproduction and juvenile survival, but not in adult survival.

It is possible that the declines in reproduction and juvenile survival were caused by factors other than increased density. However, there is no reason to suspect that conditions declined in Mokoia – e.g. monitoring of hihi (*Notiomystis cincta* Du Bus) on Mokoia from 1994 to 1998 showed no decline in reproduction or juvenile survival (Armstrong *et al.* 1999). Density dependence is the most plausible explanation for the observed trends in the saddleback population, and population models incorporating density dependence gave accurate projections. Banding was discontinued in 1997, so the subsequent growth of the population cannot be assessed accurately. However, an additional survey in 2002 recorded 177 birds, in comparison to

Table 4. Models for predicting adult survival (probability of a bird > 9 months of age surviving 12 months), juvenile survival (probability of surviving for 9 months after fledging) and mean number of young fledged per pair per year. $\phi.$ means constant survival, and ϕ_d means survival declines with density (number of pairs at the start of the breeding season). $a_p + t_2$ means the mean number of young fledged depends on the number of age 1 + birds in the pair (a_p), and on territory quality ($t_2 = 1$ for locations occupied the first year after reintroduction, $t_2 = 0$ for locations occupied later). $a_f + t_2 + d$ means that a linear decline with density is also included

	(a) Best model		(b) Plausible alternatives	
	Model	Estimate	Model	Estimate
Adult survival	$\phi.$	0·89	ϕ_d	$(e^{\beta}/(1-e^{\beta}))^{12}$ where $\beta = 5{\cdot}4 - 0{\cdot}018d$
Juvenile survival	ϕ_d	$(e^{\beta}/(1-e^{\beta}))^{9}$ where $\beta = 4{\cdot}1 - 0{\cdot}024d$		
Fledglings/pair	$a_p + t_2 + d$	$1{\cdot}26 + 1{\cdot}11a_p + 1{\cdot}16t_2 - 0{\cdot}0094d$	$a_p + t_2$	$0{\cdot}76 + 0{\cdot}99a_p + 1{\cdot}36t_2$

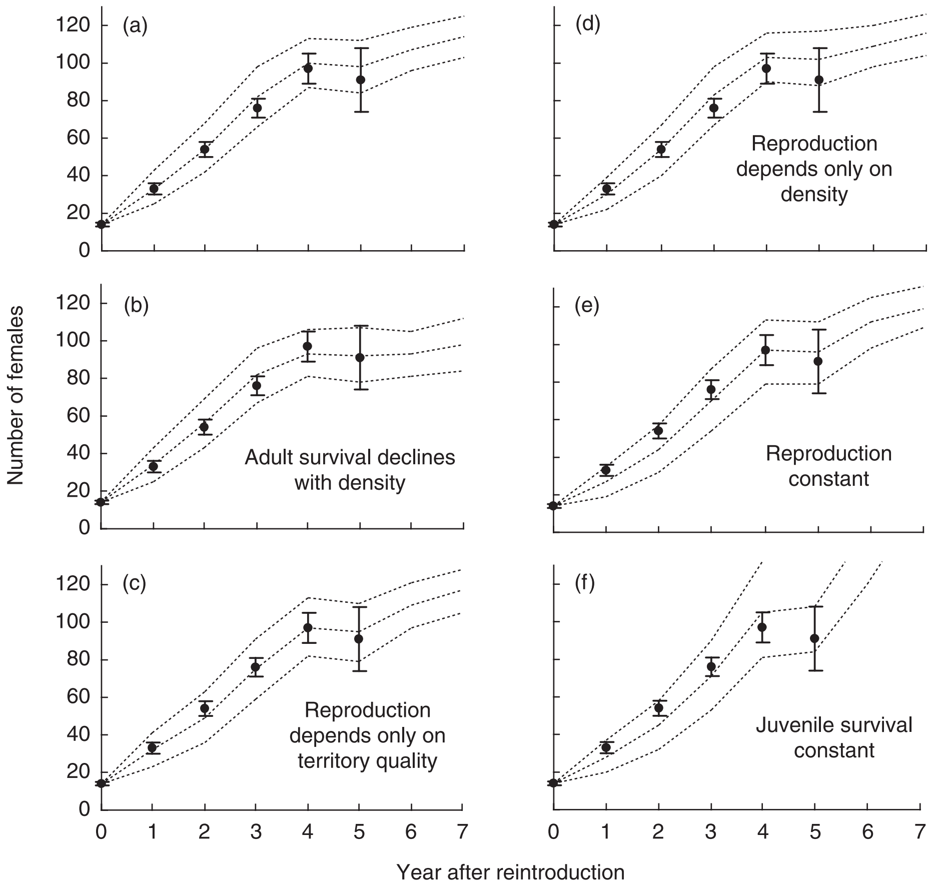

Fig. 5. Predictions of stochastic simulation models in comparison to the observed growth of the Mokoia Island saddleback population. The models include a 32% reduction at the start of year 5 to simulate the effect of the poison drop. Points show estimated numbers of females (± SE) at the start of each breeding season, the middle dotted lines show the mean numbers from simulations, and the upper and lower dotted lines show the 97·5% and 2·5% percentiles from simulations. (a) Best model, where juvenile survival declines with density and reproduction depends on territory quality and density (Table 4a); (b) as for best model but adult survival modelled as $\{\phi_d\}$ (Table 4b); (c) as for best model but reproduction modelled as $\{a_p + t_2\}$ (Table 4b); (d) as for best model but reproduction modelled as $\{a_p + d\}$, where mean fledglings/pair = 1·68 +1·31a_p – 0·015d; (e) as for best model but reproduction modelled as $\{a_p\}$, where mean fledglings/pair = 0·97 + 1·16a_p; (f) as for best model but juvenile survival probability constant (= 0·59).

150 in September 1996, consistent with our prediction that the population would stabilize slightly above the level reached in year 4 (Fig. 5).

Our results are consistent with Einarsen's (1945) classic study of pheasants (*Phasianus colchicus* Linnaeus) introduced to Protection Island. Einarsen (1945) estimated that the pheasant population rose to over 1300 in 5 years, but that the relative growth rate declined each year. This trend is based on population estimates alone. However, subsequent studies of colonizing bird populations also suggest density dependence (e.g. Harris & Wanless 1991; Nicoll *et al*. 2003; Nummi & Saari 2003), and these studies were conducted over 15 + years and included vital rates as well as density. Long-term studies of bird populations recovering from hunting (Cooch *et al*. 1989; Francis *et al*. 1992; Williams *et al*. 1993) or pesticide use (Wyllie & Newton 1991) also suggest density-dependent declines in vital rates.

It is therefore not surprising that density dependence would occur in an island population of saddlebacks in the absence of predators. What is more important is that density-dependence could be detected from a relatively short-term study (5–6 years), and that parameters declined each year after reintroduction (Figs 3, 4). It is often suggested that long-term data sets are needed to detect density dependence (e.g. Godfray & Hassell 1992; Nummi & Saari 2003). Such data sets are clearly needed if working from density estimates alone (Shenk, White & Burnham 1998), but may not be needed with good data on vital rates. Ray & Hastings (1996) found that study duration was not a major factor affecting detection of density dependence in insect populations, and was insignificant in populations with little spatial structure. Mokoia saddlebacks have no population structure in that a juvenile can disperse easily to any part of the island. The closed nature of the island also makes it easier to detect density dependence because it is unnecessary to separate statistically emigration from mortality (cf. Altwegg *et al*. 2003). Most importantly, the small size of the island (135 ha) and rapid growth of the species meant that resources could rapidly become limiting.

A key factor for detecting density dependence in reproduction was taking age into account. First-year birds produced far fewer fledglings than older birds, and the proportion of first-year birds was highest in the second year after reintroduction. If age is ignored, reproduction appears to be lowest in the second year and unrelated to density. However, age-specific reproduction declined each year, with a clear correlation with density (Fig. 4). Age distribution is expected to change in any expanding population subject to density dependence (Cooch *et al*. 1989), so must be accounted for.

We considered two models of density-dependent reproduction: (1) reproduction of all birds declines as density increases and (2) reproduction remains constant for each territory, but more birds occupy poor territories as density increases. These models are forms of scramble and contest competition (Nicholson 1954), respectively. Both (1998) referred to them as the individual adjustment hypothesis (IAH) and habitat heterogeneity hypothesis (HHH), and found his data for great tits (*Paurs major* Linnaeus) supported the IAH. Data from Spanish imperial eagles (*Aquila adalberti* Brehm: Ferrer & Donazar 1996), griffon vultures (*Gyps fulvus* Hablizl: Fernandez, Azkona & Donazar 1998) and mute swans (*Cygnus olor* Gmelin: Nummi & Saari 2003) supported the HHH, with the first sites colonized found to support higher reproductive success. Our data supported a combination of both models (Fig. 4). The key factor was the distinction between primary territories (occupied in the first year) and secondary territories (HHH), but the best model also included a linear decline on all territories (IAH). The primary territories were flat areas near the lakeshore or covered a mixture of ridge and gully habitat, whereas the later territories occupied were steeper and/or did not have the same habitat diversity.

A linear decline alone was not only a poor predictor of the productivity of individual pairs, but also a relatively poor predictor of the trend in mean productivity (Fig. 4). This makes it harder to extrapolate the model to other locations. That is, while it is easy to apply the linear model to new locations, modelling the effect of territory quality requires detailed knowledge of the habitat. However, we found that changing the form of density dependence in reproduction, or removing it altogether, made little difference to projected population growth (Fig. 5).

The key to projecting the growth of the Mokoia saddleback population was including density dependence in juvenile survival, and failure to do so increased substantially the projected equilibrium population size. We considered only one model of density dependence in juvenile survival: a linear relationship between the number of female at the start of the breeding season and the log-odds of the survival probability (the log-odds is the inverse of the logit link used in MARK). Armstrong & Ewen (2002) found New Zealand robins (*Petroica australis* Sparrman) showed a density-dependent decline in juvenile survival after reintroduction to Tiritiri Matangi, and that 5 years of data were insufficient to distinguish among models of density dependence. However, additional data allowed several models to be compared and showed the number of pairs at the start of the breeding season to be the best predictor (Dimond 2001).

Our results suggest that if researchers want to predict dynamics of bird populations, they need to assess density-dependence in juvenile survival. However, research on density dependence in birds has focused on reproduction, presumably because it is easier to study. Of 57 studies of density dependence in birds listed by Newton (1998: Table 5.1), 41 assessed aspects of reproduction and six assessed recruitment to the adult population. Estimates of recruitment are sufficient in principle to model dynamics of populations, and do not require birds to be banded until they reach adulthood. However, estimates of recruitment and density are not independent, raising the statistical problems already discussed. Unless researchers are guaranteed long-term data sets, they need to mark dependent young individually so they can estimate juvenile survival. However, the additional problem for mainland studies is that juvenile mortality is difficult to distinguish from emigration, and both are likely to change with density. This problem can potentially be overcome by combining data for resightings and dead recoveries (e.g. Altwegg *et al*. 2003). However, closed island systems provide the best opportunity to estimate juvenile survival.

Data from island populations in New Zealand can be applied to mainland reintroductions, and our saddleback model is currently being used for this purpose. These reintroductions will be to managed 'mainland islands' (Saunders & Norton 2001), which are open systems in that species such as saddlebacks may disperse from them. However, they are islands demographically in that there will be no immigrants and any emigrants will be lost to the unmanaged surroundings. The model is being used initially to predict the number of birds that can be sustainably harvested from islands, and the level of predation that reintroduced populations on the mainland can withstand (Davidson 1999). Post-release data on vital rates can then be incorporated to assess population viability under the existing management.

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