Population Dynamics of the Saddleback Population on Mokoia Island and Implications for reintroduction to the mainland

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Abstract

The saddleback (*Philesturnus carunculatus*) is an endemic New Zealand forest bird that no longer occurs on the mainland. It is thought that predation from introduced species (especially rodents) led to its extinction except on offshore islands. In April 1992, 36 saddlebacks were released onto Mokoia Island, a 135 ha island in Lake Rotorua. Using data collected from this population over the following five and a half years, I estimated parameters to describe the population's demography.

Survival was modelled by mark-recapture analysis, using re-sighting data for banded birds. Survival was found to be age dependent, with two classes, adult and juvenile. The juvenile age class consisted of birds in their first nine months. All other ages were treated as adult. Adult survival was density independent, while juvenile survival was density dependent. The juvenile survival rate was initially close to the adult rate, but declined as the number of pairs on the island increased. There was a male bias in the sex ratio of birds surviving their first nine months, but the cause for this was not ascertained.

Reproductive success was related to the age of the parents, with two classes for both males and females. For both sexes, first year breeders produced fewer fledglings than older birds. A density dependent decline in the population's reproductive success was also found.

Using parameter estimates that took these factors into account, I created a model to simulate the Mokoia Island saddleback population. My model predicted a mean population growth trajectory that closely matched the observed population growth on the island. After the establishment phase (a period of rapid growth) the simulated population reached a mean density of 103 pairs, with 44 unpaired males, around which the population fluctuated.

Once the basic model structure had been established, I added a routine to simulate the poison drop that occurred on island in September 1996. Using mark-recapture analysis, I estimated that the poison drop killed 27% of the birds. However, the simulations model predicted that this mortality would not affect the population's viability.

I altered the model structure so that effects of predation could be included, to simulate a reintroduction onto the mainland. I also added annual and biennial poisoning regimes to see if these could be used to counteract the effects of predation, and at what predation levels they would prove beneficial to the saddleback population. To do this I assumed that a poison drop would result in no predation for six months, then predation would return to normal levels. Annual poisoning was better at increasing the population's viability than biennial poisoning, but neither allowed the population's persistence at predation levels that would probably occur on the mainland.

I also looked at the effects of harvesting the island population, to see what the maximum sustainable rates were. The results from this indicated that the up to 139 birds could be harvested from the population at a single occasion without affecting population's viability, if the population was left to recover afterwards.

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Introduction

1.0 Scene Setting

Much of New Zealand's native forest has been cleared for anthropocentric uses, leaving only scattered islands of bush within a sea of pasture. With this destruction of habitat and the introduction of exotic predators, much of New Zealand's indigenous wildlife has become endangered. Management of these species is now essential for their continued survival.

About 85% of New Zealand was covered by forest before the first waves of Polynesian settlement some 700-800 years ago. When Europeans began settling New Zealand the forest cover had been reduced to 53%. At this time tussock grassland expanded from 5% to 30% coverage. Since European settlement the forested area has undergone further reduction and degradation until the present day, leaving about 23% of the land area under native forest (Taylor and Smith, 1997). Most of our remaining native bush is in areas where it was inaccessible to loggers. So as well as being heavily reduced from its original size, our native forest has become much more fragmented, with many populations of endemic species now isolated. Of the 93 endemic vertebrate species that existed in New Zealand prior to human settlement, about 50 species have become extinct (Wilson, 1997).

Most of our conservation effort has been directed towards our offshore islands where predators were either not introduced or can be removed. However, there is now a growing emphasis towards mainland conservation and restoration. Six mainland islands have been established as areas for intensive management, and there are various fragments that are managed for the survival of specific species. As these reserves are managed, there is an increasing potential for the reintroduction of native species into these areas, especially as management techniques improve. These reintroductions will pose particular challenges, as it is unlikely that all exotic predators can be eliminated, especially mustelids and rats. However, through control, they may be reduced to population densities compatible with the coexistence of native species.

Caughley (1994) suggested that there are two contrasting paradigms in conservation biology for the management of threatened species, the declining population paradigm, and the small population paradigm. The small population paradigm details the risks to small populations: demographic, environmental, and genetic stochasticity, and catastrophes. This is important for conservation as often, endangered species are located in small, isolated populations.

The declining population paradigm is the theory describing the causes of a species decline, e.g. the introduced predators and habitat destruction which has occurred in New Zealand. Diamond (1989) studied recent extinctions and found that the agents of decline could be placed into four groups: overkill, habitat destruction and fragmentation, impact of introduced species, and chains of extinctions, which he called the evil quartet. Overkill is the excessive hunting of a species above its maximum sustainable harvest. Habitat destruction and fragmentation is the result of land clearance and alteration caused through a change in land usage, such as the removal of forest and its subsequent replacement by pasture. Introduced species present new competition for indigenous species by competing with them for resources, or predation. Chains of extinction are the secondary extinctions where species react to a loss of others that they are dependent on. All of these causes of extinction have functioned and are functioning in New Zealand.

The small population paradigm is the theory of how small populations become more vulnerable to stochastic factors. Small populations are less likely to survive in highly variable environments. A small population is also much more at risk to demographic stochasticity. Small populations will lose a portion of their genetic variability depending on how small a bottleneck they pass through. Catastrophes always represent a threat to any population, but a small population can ill afford to lose members. These are all-important considerations when managing a threatened species.

These two paradigms are by no means mutually exclusive (Hedrick *et al*, 1996), and need to be melded as the agents of the decline are likely to still be affecting the small remnant populations. Both paradigms are equally relevant if a species is going to be released onto the mainland, as in most cases, the cause of the populations initial decline (e.g. predators), will still be present, and the populations that will be established will be small requiring some management.

In this thesis I am going to look at the possibility of reintroducing the saddleback onto mainland New Zealand. This species is restricted to offshore islands (except for the Mokoia Island population in Lake Rotorua), where introduced predators have failed to establish or have been eradicated.

1.1 Reintroductions

Reintroduction is defined as an attempt to establish a species in an area which was once part of its historical range, but from which it has been extirpated, or become extinct (IUCN, 1998). Animal reintroductions are carried out to increase the numbers of an endangered species by releasing them into environments where they are thought to be able to survive (Griffith *et al*, 1989; Kleiman, 1989; Stanley-Price, 1989). However failures are not often reported (Short *et al.*, 1992), and it could be said that it is common practice in management to bury the failures as quickly as possible (MacNab,1983). However when this happens nothing is gained from the exercise, and the mistakes of the past may be repeated. Southgate (1994) defines a failed reintroduction as one from which no useful information is produced to assist in the long-term conservation of a species.

It is important to have an overall plan for the conservation of a species and for each reintroduction to form a stage in that plan, rather than to act haphazardly as opportunities arise (Foose, 1991; Short *et al*, 1992; Saunders, 1994). There must be an overall strategy. The random reintroduction of a species as habitat becomes, available with no thought to the wider picture, will not benefit the species. Most successful re-establishments rely on comprehensive information on the species biology with insights into how the animals-behaviour can be manipulated or used to advantage (Stanley-Price 1989).

Reintroductions into the core of a threatened species former range are considered more likely to succeed than introductions elsewhere (Griffith *et al.*, 1989; Lawton, 1993). However, a species may be more likely to be found on the extremes of its former range (Lomolino and Channel, 1998), particularly if that area is less suited to the agent of decline (Caughley, 1994). For a reintroduction to be a success, the cause of the decline must be removed or controlled so that the population can establish and become sustainable.

1.2 The Saddleback

The saddleback is a member of the family Callaeatidae (the New Zealand Wattlebirds, Figure 1.1), that contains two other species: The huia *(Heterolocha acutirostris)* and the kokako *(Callaeas cinera)*. The huia is presumed extinct, with the last confirmed sighting occurring in 1907, while the kokako is endangered but continues to persist on the mainland. The saddleback is now restricted to island populations.

The Saddleback can be further subdivided into two subspecies the North Island *(Philesturnus carunculatus rufusater*), and the South Island *(Philesturnus carunculatus carunculatus*). The South Island saddleback juvenile has brown plumage, whereas the juveniles of *P.c. rufusater* have plumage resembling an adult. *P.c. carunculatus* adults have a gold band at the back of the shoulder, which is not found in *P. c. rufusater*.

Class	AVES
Sub-class	NEORNITHES
Infraclass	NEOAVES
Parvclass	PASSERAE
Superorder	PASERIMORPHAE
Order	PASSERIFOMES
Suborder	PASSERI
Superfamily	CORVIDEA
Family	CALLAEATIDAE

Figure 1.1. Saddleback Classification (from Sibley and Monroe, 1990).

The saddleback is a medium sized passerine about 25 centimetres in length weighing from 70 grams (females) to 90 grams (males) with the South Island subspecies weighing slightly more on average than the North Island (Jenkins, 1978). The saddleback nests in tree cavities, rock crevices, sheltered areas beneath tree fern fronds, and at the bases of bushes. Eggs are usually laid from October through to January. However, at some newly colonised sites where resources are effectively unlimited the birds can begin laying as early as August and continue through to May with up to three broods being raised (Heather and Robertson, 1996, Rasch and McClelland, 1993; this study). The most common clutch size is two (Lovegrove, 1992; this study) but broods of up to four have been recorded (Craig, 1994). Their diet is mainly invertebrates, but this is supplemented with fruit and nectar when in season (Atkinson and Campbell, 1966).

The Saddleback no longer occurs on the mainland, where it once was common (Buller, 1888). It has been unable to survive the attentions of predators that have been introduced into New Zealand with human settlement. The species was restricted to two offshore island populations, Hen Island in the north (North Island Saddleback), and the Big South Cape Islands in the south (South Island Saddleback, Fuller *et al.*, 1978). Buller (1868) mentions the declines in many native New Zealand species, though he does not identify the causes except to suggest that some are the result of human activity.

Saddlebacks were recorded at Kaitaia in 1878, Cuvier Island in 1878, Great Barrier

Island in 1882, although they had disappeared by 1900 (Oliver, 1955). They were very scarce on the mainland by the late 1880's (Buller, 1888). By the turn of the century the only substantial population of the North Island subspecies was on Hen Island, although a pair was spotted in the Raukumera Range in 1941 (Merton, 1965; Jenkins, 1976).

Introduced predators have been linked to declines in native species (Moors, 1985; Buckle and Fenn, 1992; McLennan, 1996; Wilson *et al.*, 1998). The greatest threat to the long-term survival of saddlebacks is the introduction of rodents to any of the islands where saddleback populations occur. An example of this is the ship rat eruption on Big South Cape Island in August 1962, which caused the local extinctions of several native species including the South Island saddleback (Bell, 1978). However, translocations of survivors from the island allowed populations to be established on rat free islands, preventing the complete extinction of the species. Today the South Island saddleback thrives only on rat free islands (Lovegrove, 1996), while kiore may not prey on adult saddlebacks or on juveniles, it may predate on newly hatched chicks (Atkinson, 1978). There has been only limited success with translocations to islands where this is the only rat present (Roberts, 1994). The North Island sub-species co-exists with kiore on several islands (Lovegrove, 1996b), but no reintroductions have been successful on islands inhabited by the other species of rats, except where the rats have been subsequently eradicated.

There were several releases of North Island saddleback to Kapiti Island (1981-1987) which at the time had populations of the Norway and Polynesian rats. Saddlebacks were though to be able to co-exist with these species, but the population was not self sufficient with the levels of rat predation that occurred (Lovegrove 1988; 1992). However, with the recent rat control program on this island it is likely that the surviving population will expand. The North Island saddleback is not thought to co-exist with the ship rat or the Norway rat, whereas the South Island subspecies may not be able to co-exist with any of the three rat species (Lovegrove, 1996b).

Most releases of saddlebacks with a balanced sex ratio on predator free islands have been successful (Lovegrove, 1996b). Others have probably failed because either, predators were present or arrived after the translocation, or possibly because too few birds were released. Saddlebacks have several characteristics that enable to be more likely to successfully establish (Lovegrove, 1996a):

1) Broad habitat requirements, from shrub land to tall forest.

2) A high reproductive rate. In stable established populations the saddleback normally has a low breeding productivity, but in newly established populations the population can expand rapidly.

3) Flocking behaviour that may facilitate pair formation.

4) Small territories of less than 0.4 ha on Cuvier (Lovegrove and O'Callaghan, 1982). Larger territories of up to 4 ha have been recorded in newly established populations with a lower population density (Pierre, 1999; this study).

The broad habitat requirements of the species were demonstrated by the release on Tiritiri Matangi, where there were only a few strands of old forest, with the rest of the island only recently revegetated. The saddleback does well on this island, showing that its habitat requirements were not as narrow as had been thought (Craig, 1994).

The Saddleback was released onto Mokoia Island in April 1992. The founder population consisted of 36 individuals sourced from Tiritiri Matangi Island. The population prospered on this island, it has grown to over 200 individuals by 1997.

1.3 Mokoia Island

Mokoia is a small 135 ha island in the Lake Rotorua (38° 05' S Lat.; 176° 17' E Long) which attains a height of 156 m above the lake level which is 451 m above sea level (Figure 1.2). It is the largest inland island in New Zealand and the shortest distance to the mainland is 2.1 km. This island has had a long history of human habitation and is highly modified. Mokoia Island has been revegetating for about 40 years, and there is a well developed secondary growth (Armstrong and Van Essen, 1996). The vegetation on Mokoia Island consists of regenerating secondary forest species, dominated by mahoe (*Melicytus ramiflorus*), kohuhu (*Pittosporum tenufolium*), five finger (*Pseudopanax arboreus*), and mamaku tree ferns (*Cyathea medullaris*) which dominates the canopy on the southern side. On the northern side of the island, cabbage trees (*Cordyline australis*) are abundant (Beadle, 1990). In most places the vegetation is thick, making movement difficult without tracks.

Other native bird species that have been released onto the Mokoia Island have been hihi (*Notiomystis cincta*, released in 1994) and North Island robins (*Petroica australis longipes*, released in 1991).

The last large mammals were removed from Mokoia Island in 1996, and a poison drop (brodifacoum) was carried out to eliminate mice (Mus musculus) and Norway rats (*Rattus norvegicus*) which were present on the island in low numbers.

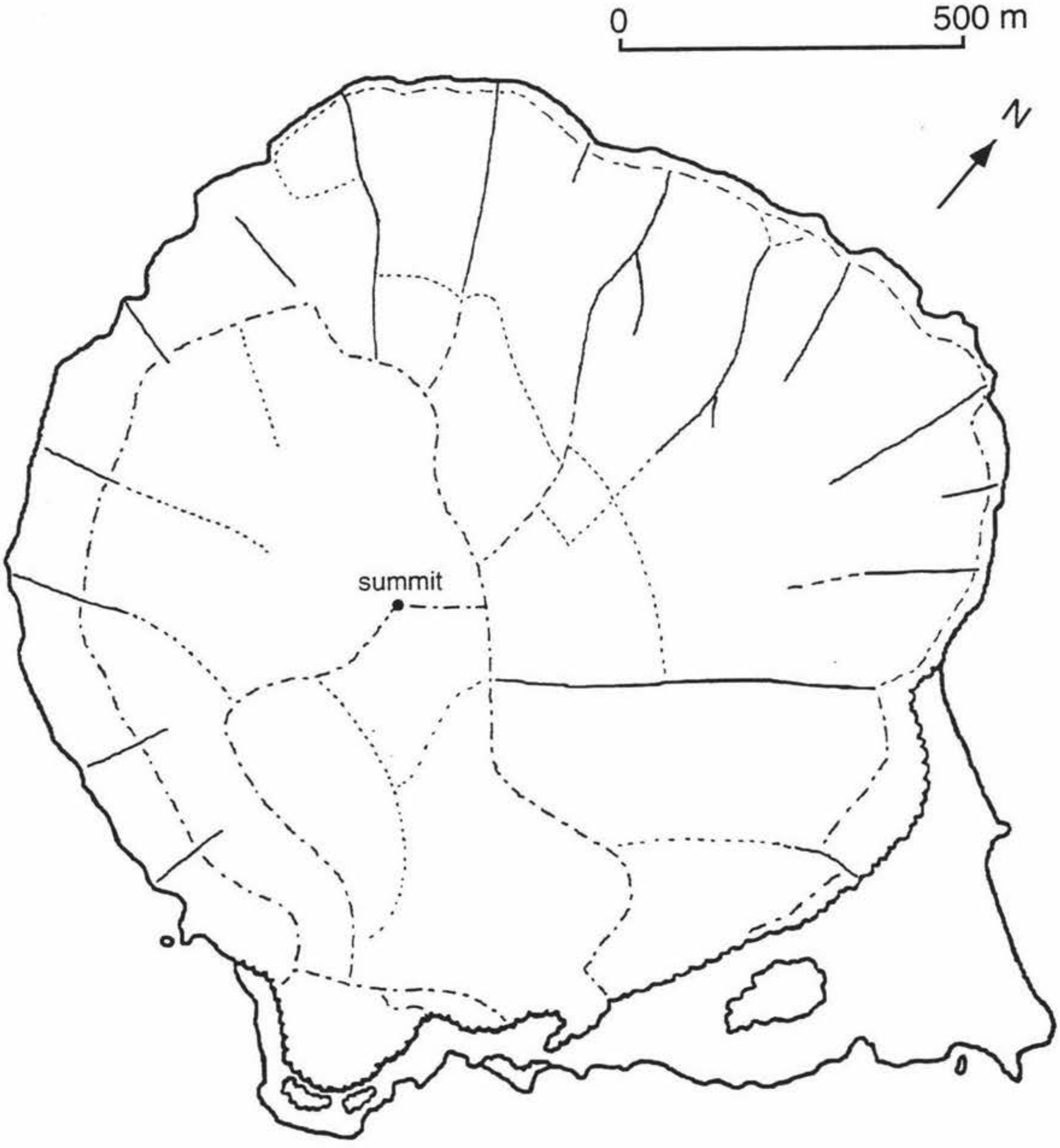


Figure 1.2. Mokoia Island in Lake Rotorua, showing tracks (broken lines), gullies (solid lines orientated towards the summit, and the forest edge. The forest is at various stages of regeneration, and consists mainly of common broadleaf species. The area outside the forest edge is mostly grass and blackberry. The summit is 156 m above lake level. (D.P. Armstrong produced this map).

1.4 Objectives of this Thesis

For my thesis, I constructed a simulation model of the saddleback population on Mokoia Island using the data collected over the period 1992-1997. The trends from these data will be extrapolated to predict the future size of the population. I will then add to the simulation model the data on the effects of the brodifacoum poison drop in September of 1996, and use this to explore some possibilities for potential mainland reintroduction. This will consist of looking at the effects of predation on survival and reproduction and whether or not poison drops are likely to increase the possibility of a mainland reintroduction succeeding.

This will be carried out in stages

Chapter 2: Saddleback Demography

I identify those parameters that are needed to construct a simulation model of the population, by analysing the data on reproduction and survival.

Chapter 3: The Model

I construct a simulation model, and perform a sensitivity analysis to identify which parameter estimates have the greatest effects on the model.

Chapter 4: Population Management

I add the effects of the poison drop to the model, and explore of the possibilities for mainland reintroduction. I aim to see if the additional mortality caused by the poison for the saddleback is overshadowed by the benefits of reducing the predator populations.

2

Saddleback Demography

2.0 Abstract

In this chapter I analyse the demographic data from the North Island Saddleback population on Mokoia Island. These data were collected over the first six years since the population was reintroduced in 1992. My goal was to estimate parameters that were used to construct a model simulating the population dynamics (used in Chapter 3).

Reproductive success, measured as the number of fledglings per pair, per year, was modelled using General Linear Modelling. Reproductive success was found to depend on both male and female age (lower for first year birds), and declined over time in proportion with increasing population density. Taking these factors into account, there was also a significant difference among pairs, which I refer to as "pair quality".

There was a male bias in the sex ratio of birds surviving to one year of age. Sexes were unknown before then, hence it is unknown whether the sex ratio at birth, or a subsequent difference in survival caused this bias.

Survival was modelled using MARK, a program for the analysis of mark recapture data. Juvenile survival (survival to nine months) declined with population density. Adult survival was density independent, and remained relatively constant over the period of the study. Adult males and females had similar survival rates.

A poison drop on the island of the anti-coagulant brodifacoum was also included in the survival analysis. There was a substantial decrease in survival during the month after the poison drop, and this was taken into account when estimating the normal population parameters.

2.1 Introduction

To create a model simulating the dynamics of the Mokoia Island population, I first needed to develop models predicting birth and death rates under the range of circumstances that were likely to be encountered. The data from Mokoia Island began with the translocation of 36 banded birds (about 16 females and 20 males) removed from Tiritiri Matangi Island in April 1992. Some of the birds were of known sex and age, having been banded as fledglings on Tiritiri Matangi Island. For the remaining birds, gender was estimated from tarsus length, which is a good predictor of sex in the saddleback (Jenkins and Veitch, 1991). The age of these birds was assessed from the plumage as the North Island saddleback has a gold band on the back, which is absent in first year birds (Jenkins, 1976). The saddleback is a cavity breeder, which can have up to three clutches a year (Heather and Robertson, 1996, Rasch and McClelland, 1993). The species is territorial, and these are maintained during the year (Jenkins, 1976), although the territory size varies with season (O'Callaghan, 1980).

The population was surveyed usually every two to six weeks from April 1992 to November 1997, with surveys carried out more frequently in summer (which was the breeding season) than in winter. There were 75 surveys of the island carried out in total. Data on the reproductive success of individuals in the population was collected during the breeding seasons 1992-93, 1993-94, 1994-95, 1995-96, and 1996-97.

Reproductive success was measured for all pairs in the first three seasons and from a sample of 31 pairs in 1995-96 and 26 pairs in 1996-97. Reproductive success was measured by observing pairs, checking nest boxes (all monitored birds had nest boxes in their territories), and looking for natural nests. When the location of a nest site was known, chicks were checked until at least two weeks old, and were then counted as fledged if they reached that age. Saddleback chicks fledge at about four weeks of age. However, a large number of nests were monitored through to fledging age, and no mortality or disappearances occurred between two and four weeks.

For birds nesting in unknown sites, the number of young with their parents was counted after fledging. Fledglings stay with their parents for at least six weeks after fledging, and all monitored birds were observed sufficiently frequently that no young would reach independence undetected. Once a pair had been found, it was simple to detect whether fledged young were present. However, because some of the fledged young died before their parents were observed, these counts slightly underestimate the number of young fledged. Parents with young from known nests were observed on the same schedule, and these data are used to estimate the proportion of young dying before their parents were observed (see below).

Re-sighting data were obtained by traversing the island during a three-day period, recording all banded birds that were seen. All young from known nest sites were individually colour banded. There were 36 banded original birds released on Mokoia, 34 in the 1992-93 cohort, 35 in the 1993-94 cohort, 72 in the 1994-95 cohort, 52 in the 1995-96 cohort, and 52 in the 1996-97 cohort, hence, a total of 281 banded birds in the study. Traversing the island involved walking along all tracks and major gullies and investigating all saddlebacks that were heard. Saddlebacks call loudly and frequently

(O'Callaghan, 1980), and any bird giving a territorial call could be heard from some point of the sampling route. Hand claps and a tape-recorded saddleback call were used to elicit responses, particularly in places where no saddlebacks were known to occur. The island could be covered twice in three days.

As well as recording whether banded birds were seen during the breeding season, the locations of all birds, whether banded or unbanded, was mapped. There were few pairs with both members unbanded, so it was easy to distinguish pairs. The total number of pairs counted during the breeding season was used as a measure of population density. This was used to test for density dependent changes in survival and reproduction

2.2 Analysis of the reproductive data

2.2.1 Methods for Reproductive data analysis

Each row of the reproductive data set consisted of records of the year, the pair, the pair's location, the age of the male, the age of the female, the number of years the pair had been together, the population size that year (observed number of pairs), and the number of fledglings produced that year. The model used to predict the number of fledglings produced was estimated using the General Linear Model option in SYSTAT version 6.0 and S-PLUS 4.5.

As mentioned above some of the fledglings from un-located nests could have been missed due to early mortality. To correct for this, for each year I calculated the proportion of fledglings from the banded broods that were not observed as fledglings with their parent. For each unbanded brood observed, I divided the number of observed fledglings by this proportion to estimate the number that had fledged. This meant that the estimated number of fledglings produced was not a whole number for some pairs. This was not rounded off, because for most pairs this would have removed the correction factor. I did not add whole fledglings to some randomly chosen clutches because this would have affected my analysis of factors affecting reproductive success.

2.2.2 Location/settlement

The island was divided into four quarters (north-eastern, north-western, south-eastern and south western). These four quarters differed in steepness due to the position of the summit, with the north-eastern portion being the flattest, and the south-western portion being the steepest. There were no other obvious schemes with which to assign territory quality. Vegetation characteristics vary greatly on Mokoia Island, but this is mostly affected by the island's topography (Perrot and Armstrong, in press). There was a series of gullies all around Mokoia Island. These gullies have larger trees, are relatively more open, and are moister than the dense, dry scrub on the ridges.

The division of the island into quarters was a *post-hoc* division based on perceived trends (Figure 2.4). It was not possible to divide up pairs in relation to habitat as almost all pairs used combinations of gullies and ridges. As there initially appeared to be some difference in reproductive rates between various parts of the island, I also looked at the settlement of the island. Based on the simple division of the island into approximate quarters, above, I analysed the proportions of birds settling in each quarter of the island over the years 1992-97, as this could potentially affect the structure of my simulation model (produced in Chapter 3).

2.2.3 Individual variation

To incorporate individual variation into the model the effects of individual females and males were fitted to the model, both separately and together. I also decided to include a term for pairs, where each different pair in the data was identified.

Better quality individuals can be expected to have more surviving offspring than poorer quality individuals. However, it can be difficult to separate differential parental quality from the effect of territory, as territories of different quality require different levels of effort for successful reproduction (Ens *et al.*, 1992) and clutch size can vary with territory quality (Högsedt, 1980). I used pair quality as a categorical variable in the analysis, while accepting that it is confounded with territory quality. Fitting the term "pair" to the data incorporates the effects of individual variation in males and females, and in territory quality. Another potentially confounding factor that could affect the estimate of individual variation was the use of nest boxes. I tried fitting two terms in the analysis to represent this. The first was the yearly proportion of successful clutches that a female had in nest boxes. The second was the proportion of successful broods that a female had in nest boxes over all years for which she were monitored.

2.2.4 Additional terms fitted

There were several other terms that were fitted to the reproductive data to produce an accurate model. I fitted male and female age to the data, to see if reproductive success increased with the ages of the birds. I fitted the number of years that a pair had been together to see if reproductive success increased with time (although this would be correlated with the age of the birds). I also fitted density dependence to the data to see if this declined as population density increases.

In addition to these terms, I looked for interactions between some of the terms. It was possible that there would be an interaction between the ages of birds, and the density dependent decline, or pair quality and the density dependent decline. I also looked to see if there was an interaction between the ages of males and females.

2.2.5 Results from analysis of the reproductive data

The data from the five years that the reproductive data were collected show three peaks in the number of fledglings produced per pair per year, at 0, 2 and 4 fledglings (Figure 2.1). The peaks at two and four fledglings are explained by the most common clutch size for the saddleback, which is two. The peak at four fledglings produced per pair corresponds to two clutches. The peak at zero is caused by birds attempting to breed in their first season. These young birds generally only attempt to breed once in their first year, towards the end of the breeding season.

A number of models were fitted to the reproductive data using the General Linear Modelling menu in SYSTAT (Appendix A). The seven models with the highest R^2 values all included terms that were not significant, and when these were removed, the fit of the model worsened. There were two models (models 14 and 15, Appendix A) which had high R^2 values (0.9072), and in which all terms were significant. These models both fitted male and female age classes and a density dependent decline in reproductive success. However, the first model fitted individual male and female qualities, whereas, the second fitted pair quality. I decided that the best model to use was the one that fitted pair quality (Table 2.1), as I was uncertain about the accuracy of the values estimated for individual males and females (Section 2.2.3), as values were being fitted to 71 males and 70 females, rather than to just 82 pairs.

Table 2.1. Analysis of variance for the best general linear model fitted to the reproductive for all pairs. Both males and females are divided into two age classes: first year birds, and older birds. Density is the number of pairs breeding on the island in each season.

Source	Sum of Squares	D.F.	Mean Square	F-ratio	P
Density	5.3962	1	5.3962	6.6725	0.0122
Female age class	7.4643	1	7.4643	9.2297	0.0035
Male age class	5.4903	1	5.4903	6.7888	0.0116
Pair quality	252.8115	81	3.1211	5.8468	0.0000
Error	48.5236	60	0.8087		

There was a decline in the reproductive success per pair as the number of pairs on the island increased (Figure 2.2). This relationship was treated as linear because the shape can not be ascertained from five years of data.

Figure 2.1. Overall distribution of the number of fledglings produced per pair in one year. This graph is produced from all data records for the five years of the study (1992-96 inclusive). The correction factor (see Section 2.2.1) has been rounded off for this graph.

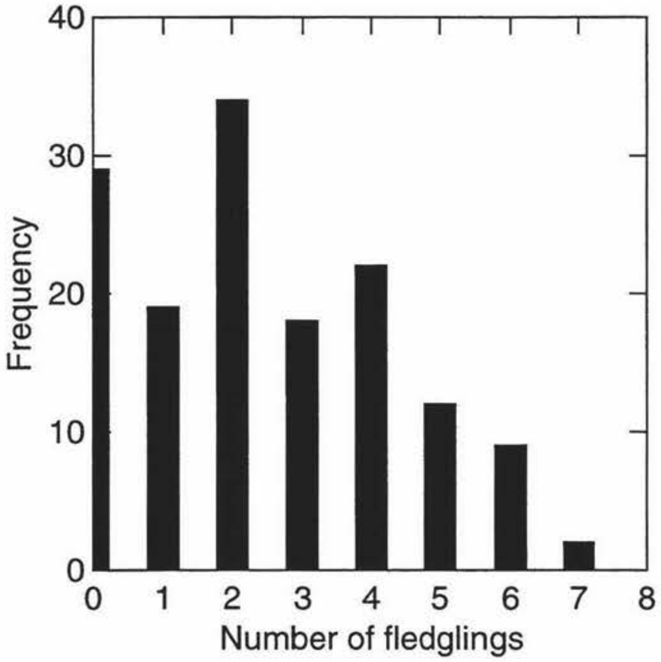


Figure 2.2. Least square means for the number of fledglings produced per pair plotted against the population density (number of pairs in the population). The least square means are taken from SYSTAT output with year fitted as a categorical variable, with male and female age classes fitted to the general linear model as well.

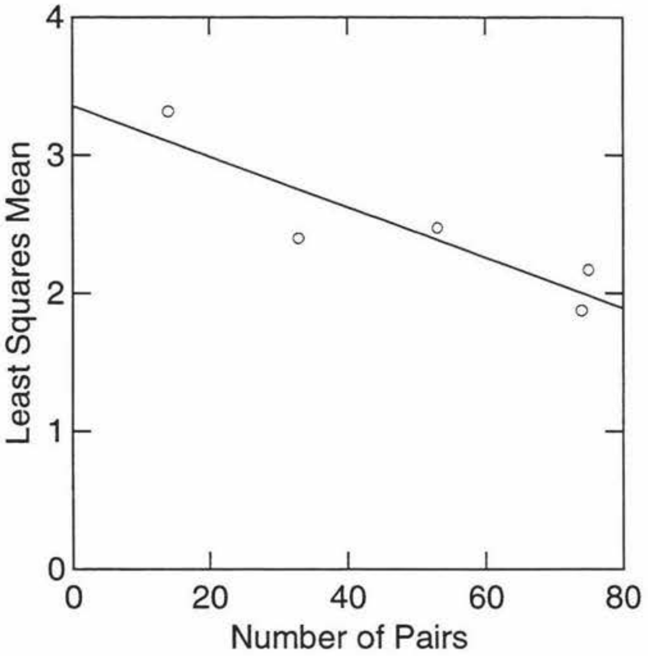
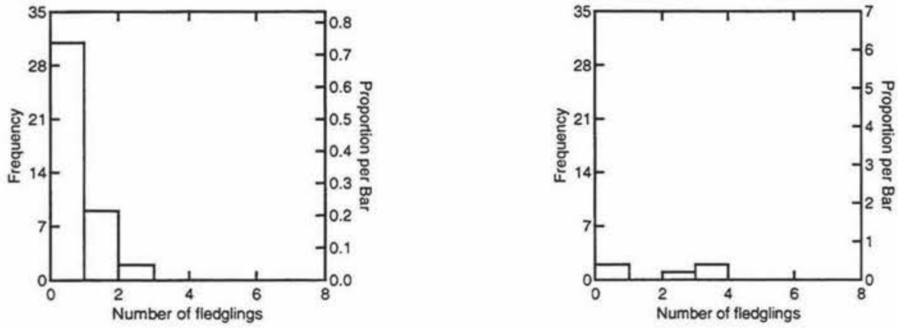


Figure 2.3. Frequency distribution of number of fledglings per pair per year with: (A) a first year male and a first year female, (B) a first year male with an older female, (C) an older male with a first year female, and (D) both birds two years or older. Data are pooled for the five years.



A. Male 1, female 1

B. Male 1, female 2.

C. Male 2, female 1.

D. Male 2, female 2.

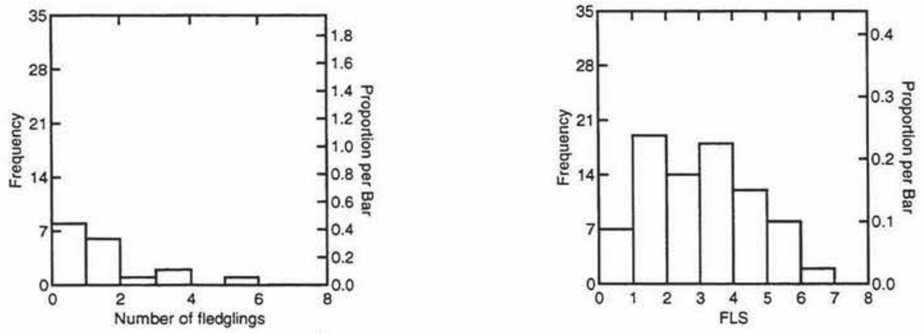
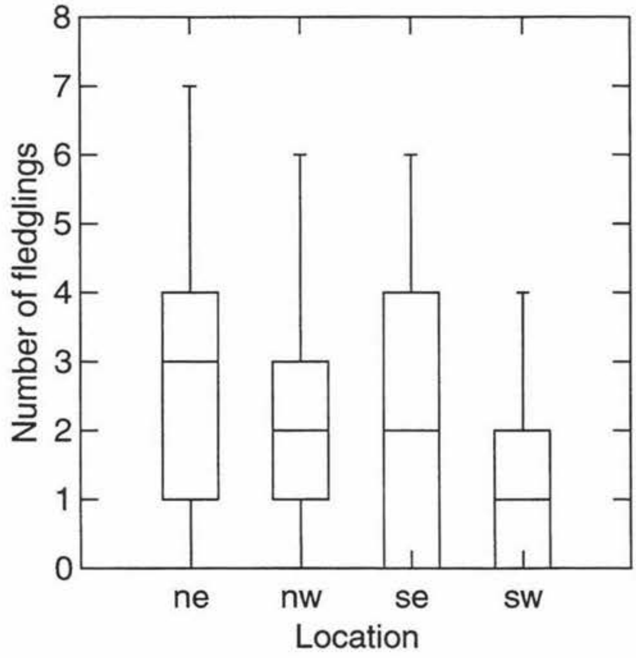


Figure 2.4. Number of fledglings per pair per year in relation to quarter of the island that the pair was located in. The island was divided into four approximate quarters along the lines of the compass (ne is the north-eastern quarter, nw is the north-western quarter, se is the south eastern-quarter, and sw is the south-western quarter).



Reproductive success was affected by the age of both the male and the female, with first year birds producing fewer young (Table 2.1, Figure 2.3). A pair consisting of one-year-old birds appears to have a maximum of 2 fledglings produced (Figure 2.3A). These birds always breed late in the season, which limits them to one clutch. There were only five pairs recorded which consisted of one-year-old males with older females (Figure 2.4B), so this distribution does not offer much information. Including interaction between age and population density, or between the male and female age classes did not improve the fit of the model (see Appendix A, models 16,17, and 21). Including either of the two terms for nest box use did not significantly improve the fit of the model, and the index of nest box use was uncorrelated with either pair or female quality.

While there was an apparent difference in reproductive success between the 4 portions of the island, before any other factors were taken into account, location did not improve the fit of the model significantly (see Appendix A, models 3, 5, 13, and 18). The differences in the average number of fledglings (Figure 2.4) were probably influenced by an uneven distribution in age groups between portions and the low sample size in the Southwest portion (9 records). The proportions of birds settling in each quarter of the island did not change significantly between years (χ^2, $P > 0.90$), so the distribution of birds does not appear to change with population density.

2.2.6 Parameter estimation for the simulated reproduction

Once the best model had been established, I needed to estimate the values for these parameters. However, there was a problem of a lack of repeated measures for some of the pairs, as of the 82 different pairs recorded in the data set, only 37 of these occurred more than once. It was necessary to use only those pairs that occurred more than once because it is otherwise impossible to separate variation due to pair quality from random error.

The parameter values were determined by fitting the variables for density dependence, male age class, and female age class to the reduced data set (omitting pairs that only occurred once) using S-PLUS version 4.5 (Table 2.2). These parameters were fitted first to gain accurate estimates of how much variation in the data set they explained. Pair quality was then fitted to the residuals from this procedure. This two tiered approach should have given more resolution in the parameter estimates than just attempting to fit them all together, as the pair quality term has the potential to affect the estimates of the other parameters because of the number of pairs fitted. The cost of fitting more terms in a regression analysis is the loss of precision in the estimates of the parameters (Cooch and White, 1998).

The value for pair quality was distributed approximately normally around a mean of 0, with a standard deviation of 1.26. This value is used as a measure of the quality of individual pairs in the population, with better quality pairs producing more fledglings. It is used in the reproductive function in the model (see Section 3.2.6).

There was a small residual left from fitting pair quality, which could be used as a measure of demographic stochasticity. The standard deviation of this value was 0.77 and it had a mean of 0. This value could be used to incorporate random variation into a pair's reproductive success from year to year (see Section 3.2.6).

Table 2.2. Parameters calculated for the reproductive equation. This table gives the values for the parameters used in the fecundity model. Parameter estimates were obtained using S-PLUS 4.5. This table gives separate estimates for first year and older males and females, although these are not estimated independently. The categorical parameters are estimated so that they sum to zero.

Parameter	Estimate	Standard error	95 % Confidence Interval	
			lower	upper
Intercept (birth)	3.23	0.42	2.40	4.06
Density dependent parameter (birth)	-0.02	0.01	0.03	0.00
Male age class (1st year)	-0.35	0.27	0.18	-0.89
Male age class (2nd + year)	0.35	0.27	-0.18	0.89
Female age class (1st year)	-1.05	0.25	-0.56	-1.53
Female age class (2nd+ year)	1.05	0.25	0.56	1.53
Intercept (birth)	3.23	0.42	-4.30	-3.08

2.2.7 Environmental stochasticity in reproduction

I also estimated the range of environmental stochasticity in the population's reproductive success for the five seasons that reproductive data were available. I did this by including a categorical term for year in addition to the other terms fitted above. This categorical variable accounted for the differences between years after the other factors (male and female age, pair quality, and density dependence) had been accounted for. These values were assumed to represent the variation due to environmental factors affecting the population. Since there were only five values (one for each year of reproductive data), I was not able to test any specific distribution for environmental variation. I assumed that it was normally distributed around the mean value given by the general linear model determined above. The standard deviation for these values was 0.202, and I used this as a measure of the environmental stochasticity in reproduction. This method does not take into account any sampling error in the values used to estimate the reproductive success of the population, so is an over estimate of the total variation between years.

2.3 Analysis of the survival data

2.3.1 Methods for the survival analysis

The survival analysis was completed using the program MARK version 1.3, developed by White (1998). Survival was modelled using the Cormack-Jolly-Seber model for live recaptures (Cormack, 1964; Jolly, 1965; Seber, 1965; Brownie, 1987; Clobert and Lebreton, 1987; Lebreton *et al.*, 1992).

The CJS model implemented by MARK allows the analysis of data with unequal time intervals. Animals recorded at time t_0 and encountered at t_1 have a survival probability of ϕ_1 for the interval between occasions and a recapture probability of p_1. The CJS model involves several assumptions that the data should fit. (1) Every marked animal present at time (i) has the same probability of being re-sighted. (2) Every marked animal in the population at time (i) has the same probability of surviving to time (i+1). (3) Marks are not lost or missed.

Marked animals are released into the population at the first occasion in the encounter record, and are then encountered at future surveys (data can be either re-sighting, or recapture records). The records of the re-encounter occasions can then be used to estimate the survival rate. For a banded animal there are three possible results from an encounter: (1) it is seen, (2) if it is not seen but is still in the population, or (3) it is not seen and is dead.

Over the five and a half years of the study there were 75 separate surveys of the island, which with the initial release gave a total of 76 encounter occasions. This was too much information for the computer to analyse, so the data set was reduced to 25 occasions (Table 2.3). These were selected to coincide approximately with March, July, September, and December, but we also preferentially selected surveys with high re-sighting rates. One extra survey (encounter occasion 20) was included to estimate the effect of a poison drop on the island on the saddlebacks. The previous survey (20-23/9/96) was conducted immediately after the poison drop (18/9/96). This was considered to be the pre-poison survey because the poison used (brodifacoum which is discussed in Section 4.1.2) is a slow acting poison that is not expected to cause mortality until several days after a lethal dose is ingested.

Table 2.3. Time between encounter occasions in months. Time is measured in months and the total length of time covered by the data set is 67 months. The occasion added to sample survival after the poison drop is number 20). The dates given are those at the start of each survey.

Date	12/4/92	10/6/92	8/9/92	20/12/92	1/4/93	28/8/93	26/10/93	25/11/93	26/3/94	13/8/94
Encounter occasion	1	2	3	4	5	6	7	8	9	10
Time between occasions	-	2	3	3	3	5	2	2	3	5
Date	3/9/94	12/12/94	2/3/95	12/6/95	16/10/95	5/12/95	28/3/96	16/6/96	20/9/96	8/11/96
Encounter occasion	11	12	13	14	15	16	17	18	19	20
Time between occasions	1	3	3	3	4	2	4	3	3	2
Date	15/12/96	17/2/97	25/6/97	5/9/97	1/11/97					
Encounter occasion	21	22	23	24	25					
Time between occasions	1	2	4	2	2					

The encounter histories of the population were stored in a file as a binary variable (100110). If a bird was seen at an encounter occasion then it coded as one. If it was not seen at an encounter occasion then it was coded as zero. There were encounter histories for 281 birds, and of these there were 172 unique encounter histories. Individuals can be divided into two or more groups in the encounter history file. During part of this analysis, two groups were specified (male and females). The analysis was performed on a Pentium II 266Mhz computer with 128 megabytes of ram, running Windows 95.

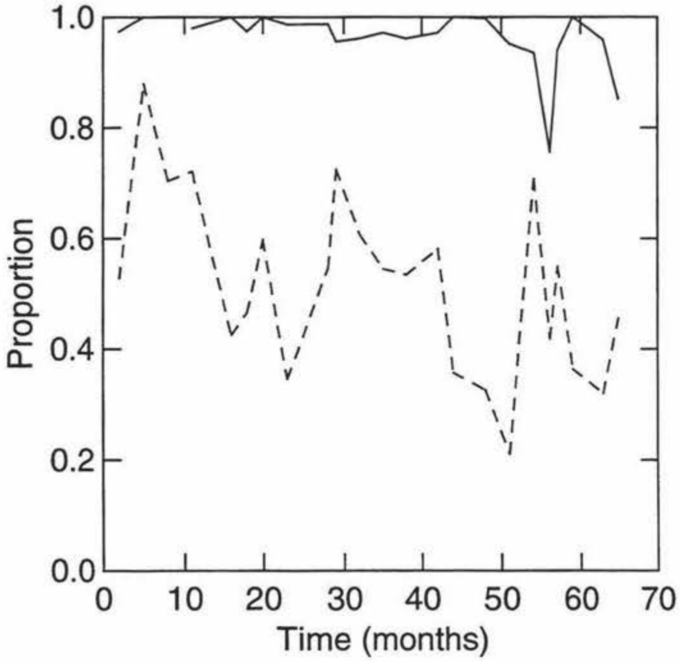
Before I began the survival analysis I used MARK to produce survival and re-sighting estimates for each encounter occasion in the data set (Figure 2.5). The large drop in survival at month 57 is associated with the poison drop that occurred in the month preceding it. These results were produced using an unconstrained CJS model (24 survival parameters and 24 re-sighting parameters).

To get the best estimates of factors affecting survival, I needed to find the simplest model that would adequately fit the data. There were a number of factors that were tested to see if they explained any of the variance in the mortality over the five years. These included, population density (number of pairs), age (adult versus juvenile), the effect of the poison drop, gender, seasons, and a possible translocation effect on survival (i.e. lower survival immediately after translocation).

2.3.2 Model fitting

Models are specified in MARK using two types of matrices: parameter index matrices and design matrices (see Table 2.4 and 2.5 for examples). These matrices allow constraints to be placed on the parameter estimates (Cooch and White, 1998). The parameter index matrices are used to code for survival and re-sighting parameters. The

Figure 2.5. Re-sighting and survival rates for the Mokoia Island saddleback population estimated by using an unconstrained CJS model in MARK 1.3. Time is measured in months from release on the island. "Proportion" is the monthly survival rate over the interval since the last encounter, or the proportion of the population re-sighted at that encounter occasion. Survival is shown as the solid line (______), and re-sighting is shown as the dotted line (----). These survival and re-sighting rates are determined for the entire population, making no distinctions for age.



survival parameters (ϕ) apply to the intervals between encounter occasions. The re-sighting parameters (p) apply to the encounter occasions. The columns in a parameter identity matrix correspond to the encounter occasions. The rows in the parameter matrix represent separate cohorts in the data set, with the first column in the row being the first encounter occasion for that cohort. By altering the numbers in the parameter index matrix, different models can be applied to the survival and re-sighting data.

In my analysis, the parameter index matrices were used to create separate survival and re-sighting parameters for adults and juveniles (Table 2.4). Each age class had a separate survival parameter coded for each interval between encounter occasions. A similar parameter index matrix was used to create the re-sighting parameters for the encounter occasions.

The design matrix is used to place further constraints on the parameter estimates, and to progressively simplify the model that is fitted to the data. It has as many rows as there are parameters in the parameter index matrixes. However, the number of columns can be fewer, and is reduced as the model is simplified. The number of parameters in the model equals the number of columns in the design matrix (White and Burnham, 1997). The program then estimates values for each column (β terms). Two different types of constraints can be applied. First, by using dummy variables (1 or 0), the parameters can be constrained to be the same for different encounter occasions, age classes, or groups. Second, using covariates, linear trends can be fitted to survival, or re-sighting rates.

In my best model (Table 2.5, Section 2.3.13), there was a covariate coding for a linear decline in juvenile survival with population density (number of pairs). Dummy variables were used to specify separate survival rates for adults and juveniles and to include the effect of the poison drop on juvenile and adult survival. Dummy variables were used to specify separate re-sighting rates for adults and juveniles, and to allow overall re-sighting rates to vary independently for each encounter occasion, but constrain the model so that the effects must be additive for age and time.

Table 2.4. Parameter index matrix used for the MARK analysis of the survival data. Numbers 45-47 refers to the first three encounter occasions for the introduced birds. Numbers 1-21 are the encounter occasions for adult birds. Numbers 22-44 are encounter occasions for juveniles. Time progresses from left to right across the matrix. Cohorts proceed down the table, with each row representing a new cohort. Birds are considered to be juveniles for their first nine months. Numbers 16 and 39 mark the point where the effect of the poison is measured. There is a similar matrix for re-sighting parameters, which are numbered 48-94.

45	46	47	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
	22	23	24	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
		23	24	25	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
			24	25	26	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
				25	26	27	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
					26	27	28	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
						27	28	29	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
							28	29	30	8	9	10	11	12	13	14	15	16	17	18	19	20	21
								29	30	31	9	10	11	12	13	14	15	16	17	18	19	20	21
									30	31	32	10	11	12	13	14	15	16	17	18	19	20	21
										31	32	33	11	12	13	14	15	16	17	18	19	20	21
											32	33	34	12	13	14	15	16	17	18	19	20	21
												33	34	35	13	14	15	16	17	18	19	20	21
													34	35	36	14	15	16	17	18	19	20	21
														35	36	37	15	16	17	18	19	20	21
															36	37	38	16	17	18	19	20	21
																37	38	39	40	18	19	20	21
																	38	39	40	41	19	20	21
																		39	40	41	42	20	21
																			40	41	42	20	21
																				41	42	43	21
																					42	43	44
																						43	44
																							44

The β terms estimated (one for each column in the design matrix) can be added to create a linear equation of the form $\beta_1 + \beta_2 + \beta_3$. This can then be used to calculate the survival or re-sighting estimate of that parameter. As the range of values from these equations can lie between –infinity to +infinity, which is the assumption for normal linear regression models, a link function was required to convert the linear equation into a probability between 0 and 1. The link function must be specified before running any model in MARK, and it determines how the β estimates are estimated. I selected the logit link function, which is the default option for any model with constraints. Using the logit link, survival and re-sighting probability are calculated by:

$$\frac{e^{(\beta_1+\beta_2 \ldots.)}}{1+e^{(\beta_1+\beta_2 \ldots.)}}$$

Table 2.5. Sample design matrix fitted to the parameter index matrix given in table 2.4. The design matrix has been split over two pages. The rows for the survival parameters (ϕ) are given on this page, and the rows for the re-sighting parameters (p) are given on the next page. This design matrix codes for the model ϕ(Pop * Ju + Age + Pois * Age) p(Age * Time) (see Table 2.7 for explanation of this notation), which was the best model. The parameter index matrix codes for a nine month juvenile stage (ϕ_{21-44}), adult survival is terms are (ϕ_{1-21} and ϕ_{45-47}). This model has density independent adult survival (β_2), and density dependent juvenile survival (β_1 and β_3). Parameter β_1 is a linear trend affecting juveniles only. The model also includes the effect of the poison drop, β_4 is the effect of the poison drop on adults (ϕ_{16}), and β_5 is the effect of the poison drop on juveniles (ϕ_{39}).

β	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
φ1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
φ2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
φ3	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
φ4	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
φ5	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
φ6	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
φ7	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
φ8	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
φ9	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
φ10	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
φ11	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
φ12	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
φ13	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
φ14	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
φ15	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
φ16	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
φ17	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
φ18	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
φ19	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
φ20	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
φ21	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
φ22	7	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
φ23	13	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
φ24	13	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
φ25	13	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
φ26	13	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
φ27	33	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
φ28	33	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
φ29	33	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
φ30	33	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
φ31	53	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
φ32	53	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
φ33	53	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
φ34	53	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
φ35	74	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
φ36	74	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
φ37	74	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
φ38	74	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
φ39	75	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
φ40	75	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
φ41	75	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
φ42	75	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
φ43	75	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
φ44	90	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
φ45	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
φ46	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
φ47	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

The re-sighting model includes age and time. The model fits time dependent re-sighting rates, where the re-sighting rate is estimated for each individual occasion (there are 24 encounter occasions), but with an effect for age. β_6 is the re-sighting parameter for adults ($p_{48\text{-}68}$ and $p_{92\text{-}94}$). β_7 is the re-sighting parameter for juveniles ($p_{69\text{-}91}$4). $\beta_{8\text{-}31}$ code for re-sighting on each encounter occasion.

β	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
p 48	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
p 49	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
p 50	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
p 51	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
p 52	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
p 53	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
p 54	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
p 55	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
p 56	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
p 57	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
p 58	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
p 59	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
p 60	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
p 61	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
p 62	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
p 63	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
p 64	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
p 65	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
p 66	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
p 67	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
p 68	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
p 69	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
p 70	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
p 71	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
p 72	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
p 73	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
p 74	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
p 75	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
p 76	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
p 77	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
p 78	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
p 79	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
p 80	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
p 81	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
p 82	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
p 83	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
p 84	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
p 85	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
p 86	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
p 87	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
p 88	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
p 89	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
p 90	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
p 91	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
p 92	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
p 93	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
p94	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

2.3.3 Model selection

The analysis of mark-recapture data rests very heavily on model selection (Lebreton *et al.*, 1992). To indicate the quality of a model's fit, MARK computes the corrected Quasi Akaike Information Criterion (QAIC$_c$). This is calculated from the formula

$$\frac{-2\log(\text{likelihood})}{\text{c-hat}} + 2K + \frac{2K(K+1)}{n - K - 1}$$

c-hat corrects for over dispersion in the data (Anderson *et al.*, 1994). This occurs where the survival or re-sighting rates are not independent among individuals. K is the number of parameters estimated. The sample size is given by n (from White and Burnham, 1997), which is 281 here. The QAIC$_c$ can be used to select the best model (Akaike, 1985).

The best model is that which has the lowest QAIC$_c$, indicating the best compromise between selecting the model that best fits the data (least deviance), and the model having the least parameters. Likelihood ratio tests can also be use to test whether the increase in deviance caused by simplifying a model, is statistically significant, which indicates that the parameters should be retained (Lebreton *et al.*, 1992). It is currently unclear whether the QAIC$_c$ or likelihood ratio tests are better criteria for model selection (Cooch and White, 1998), but the results are usually closely matched.

2.3.4 Age structure

It is dependent on the researcher to decide which values are biologically feasible and should be included in the model. It was apparent that there was some age structure in the survival and re-sighting rates, but it was not clear how juveniles should be defined. I created several different parameter index matrices specifying different schemes for specifying a juvenile period (Table 2.6). The parameter index matrices were coded to create, a three month juvenile phase, a six month juvenile phase, a nine month juvenile phase and a twelve month juvenile phase, where the survival of juveniles during that time period was estimated separately from the survival of the adults. In all cases I used the full $\{\phi(\text{Age*Time})\ p(\text{Age*Time})\}$, which estimates a separate parameter for each time interval for both adults and juveniles. The nine-month age structure produced the best model and was used in subsequent analyses (Table 2.6). This identified different survival trends between adults and juveniles (Figure 2.6), where adult survival is relatively constant and juvenile survival declines over time. The first model listed is the CJS model that produced the results in Figure 2.6.

Figure 2.6. Survival rates for adult and juvenile saddlebacks on Mokoia Island based on a nine month juvenile period (Section 2.4.4), estimated with the model {ϕ(Age*Time) p(Age*Time)} (see text). Survival is the proportion of birds surviving over the interval from the last encounter occasion. Adult survival is shown as the solid line (___), juvenile survival is shown as a dotted line (----). The dip at month 57 is due to the poison drop.

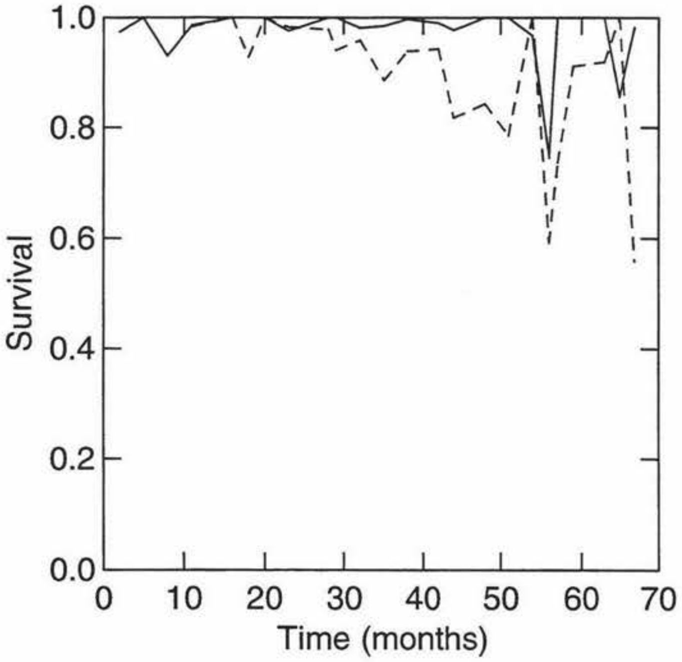


Table 2.6. Results for models fitting different age structure to the survival data. "$QAIC_c$"is the quasi Akaike information criterion score for each model. "Parameters" is the number of parameters fitted by each model. "Deviance" is a measure of how well the model fits the data. No results could be obtained when a three-month juvenile phase was modelled, but lack of convergence generally indicates a model with poor fit.

Model	$QAIC_c$	Parameters	Deviance
No age structure	3021.865	48	1941.184
Three month juvenile period	No convergence		
Six month juvenile period	2966.671	94	1768.678
Nine month juvenile period	2951.523	94	1752.274
Twelve month juvenile period	2963.906	94	1765.684

2.3.5 Goodness of fit testing

Once the age structure of the population had been established, a goodness of fit test was performed to calculate the over dispersion inflation term c-hat, which is used in calculating the $QAIC_c$ for all models. The model used for the goodness of fit is the most parameterised model, including all the parameters that are likely to be relevant for survival and re-sighting.

The model that I used for the saddleback population included adult and juvenile terms, separate density dependent declines in survival for adults and juveniles, four seasons (autumn, winter, spring and summer), adult and juvenile poison effects, and an initial effect of the translocation. The re-sighting model used was an identity matrix applied to the parameter index matrix for adults and juveniles, producing 47 β terms for re-sighting, including 24 adult re-sighting values and 23 juvenile re-sighting values. This model had a deviance of 2272.6 and 56 parameters. I did not include the effect of gender in this model, as that analysis required removing the birds of unknown sex from the data set (see Section 2.3.10).

The method for goodness of fit estimation involves a bootstrapping routine incorporated into MARK. 100 encounter histories are simulated for the data set using the parameter estimates calculated from the model being tested. The simulated data exactly fits the assumptions of the CJS model (Cooch and White, 1998). The deviances from the bootstrapping results can be use to estimate c-hat, by dividing the model's deviance by the average deviance of the bootstrapped results. I ran 100 bootstrapped simulations and these gave a mean deviance of 2089.2, with a standard error of 7.0847. All bootstrapped deviances lay between 1907.1 and 2270.2. This indicated that he probability of finding a better model than the initial one was very high ($P > 0.99$).

The calculated value of c-hat for the data was 1.08, and this value was used to alter all $QAIC_c$ scores.

2.3.6 Density dependent effects

The number of pairs was used as an estimate of density on the breeding success of the birds. An initial estimate of seven pairs was used as a feasible number that could have produced the 14 pairs that were first released on the island and 90 pairs was estimated for the 1997-breeding season. It was necessary to have the estimate of seven pairs for the 1991-92 season as density dependent declines were fitted to both adults and juveniles before the 1992-93 season.

2.3.7 Season

The possible effect of season on mortality rate was included in the analysis. Seasons were coded in the design matrix based on what the period before an encounter occasion had been. This resulted in four β terms to be fitted to the model.

2.3.8 Poison

It was apparent that survival was lower after the poison drop on Mokoia Island on 18 September 1996. The effect of the poison drop is discussed in Chapter 4. The effect is included here to remove its effects from parameter estimation.

2.3.9 Period after reintroduction

This was included in the analysis as there is commonly lower survival in the period after a translocation (Kurzejeski and Root, 1988; Slough, 1989; Lovegrove, 1992; Wilson *et al.*, 1992; Musil *et al.*, 1993). The first three encounter occasions after the release (covering 8 months) were considered to be post translocation.

2.3.10 Gender

Once I had established the best model of survival from the complete data set (treating all birds as one group, ignoring sex), I tried to fit sex into the model to see if this affected survival. The complete data set included many birds of unknown sex, which had died before their sex was known. I removed these from the data set and coded the encounter histories file to divide the remaining birds into two groups, males and females. I then constrained the model to remove the effects of sex, and compared the

Table 2.7. Models fitted to the survival data from the saddleback population on Mokoia Island. Models are in order of complexity (number of parameters). The models are listed in three groups, where either the survival or the re-sighting model remains the same, with the other being varied. The models in each group are ordered by the number of parameters in each model. The first group explores the fitting of the survival model and the second explores the fitting of the re-sighting model. The third group consists of other models that were fitted for completeness. Pop is the number of pairs in the population, and is fitted as a linear trend. Pop * Ju is this trend fitted to the juvenile age class only. Age is the age class of the individuals, either adult or juvenile. Pois is the poison effect term. Ssns is seasonal effects fitted (winter, spring, summer, autumn). Time is the 24 encounter occasions. 3pd is a term fitted to the first three encounter occasions for the post-translocation effect. "QAIC_c" is the Quasi Akaike Information Criterion. "NP" is the number of parameters in the model. "Deviance" is the measure of the models fit to the data, lower values indicating a better fit. The three best models with the lowest Qaic_c are marked in bold. The two models marked with an ! are the two models that were compared with a likelihood ratio text (see text). Additive terms are shown as + and interactions are shown with an *.

Model description	QAIC_c	NP	Deviance
ϕ(Pop * Age + Ssns + Pois * Age + 3pd) p(Age * Time)	3345.402	56	2272.582
ϕ(Pop * Age + Pois * Age) p(Age * Time)	3071.169	54	1980.384
ϕ(Pop * Ju + Age + Pois * Age) p(Age * Time)	**2881.370**	**52**	**1779.601**
ϕ(Pop * Ju + Age + Pois * age + 3pd) p(Age * Time)	2920.778	51	1824.643
ϕ(Pop * Ju + Age + Pois) p(Age * Time)	2891.988	51	1793.466
ϕ(Pop * Age) p(Age * Time)	2944.300	50	1852.477
ϕ(Age) p(Age * Time)	2977.186	49	1890.447
ϕ(Pop * Ju + Age + Pois * Age) p(Pop + time)	3192.098	31	2164.936
ϕ(Pop * Ju + Age + Pois * Age) p(Age + Time)	**2878.251**	**31**	**1825.078**!
ϕ(Pop * Ju + Age + Pois * Age) p(Pop + Ssns)	3222.468	11	2242.743
ϕ(Pop * Ju + Age + Pois * Age) p(Age)	3259.585	7	2291.737
ϕ(Pop * Ju + Age + Pois * Age) p(Pop)	3243.314	7	2274.114
ϕ(Pop * Age + Ssns + Pois * Age + 3pd) p(Age + Time)	3282.191	37	2248.719
ϕ(Pop * Age + Ssns + Pois * Age) p(Age + Time)	3087.303	36	2039.985
ϕ(Age + Ssns + Pois * Age) p(Age + Time)	2896.481	34	1837.948
ϕ(Pop * Age + Pois * Age) p(Age + Time)	3096.442	32	2054.481
ϕ(Pop * Ju + Age + Pois * Age +3pd) p(Age + Time)	**2880.037**	**32**	**1824.726**!

fit.

2.3.11 Results from survival analysis

The best model that was fitted to the data distinguished between adults and juveniles. Adult survival was modelled as density independent, whereas juvenile survival was modelled as density dependent (declining as the number of pairs increased). This model also included separate adult and juvenile poison effect terms. The re-sighting rates were separate for each encounter occasion. Differences between adult and juvenile re-sighting rates were considered to be constant over time. This is referred to as the standard model below. This model implies that adult survival will remain constant from year to year, and that juvenile survival will decline with the number of pairs in the population. A likelihood ratio test was performed on the two models with the lowest $QAIC_c$ scores, as there was only a small difference between these models. The p value from the test was 0.55, indicating that the more parameterised model, including the effect of the post-translocation period, did not significantly increase the fit of the model. While the model used for the goodness of fit testing had a high deviance compared to the bootstrapped samples, the deviances for the three best (more simplified) models are all less than the mean value determined.

2.3.12 Results for including Gender

Adding a distinction between male and female birds did not improve the models $QAIC_c$ (Table 2.8). The standard model had a lower $QAIC_c$ than the model incorporating male and female specific survival rates, and the Likelihood ratio test also supported the standard model. The deviance of the standard model differs from that given in Table 2.5 because the group effect is included, and because birds are removed from of unknown sex from the data set.

Table 2.8. Testing for differences in survival between sexes for adult birds. "Model" is the combination of factors used to predict survival. "QAIC$_c$" is the quasi-Akaike information criterion value, and is used to rank the models in descending order of best fit. "Parameters" is the number of parameters that is fitted with to model. ϕ (std) p (std) is the standard model fitted to the entire data set that was found to be the best fitting model (see Table 2.7 for definition). ϕ (std + Sex) p (std) includes the distinction between survival for male and female birds.

Model	QAIC$_c$	Parameters	Deviance
ϕ(std) p(std)	2904.72	31	2004.184
ϕ(std + Sex) p (std)	2907.34	32	2007.013

2.3.13 Survival Parameters

Table 2.9 gives the values for the survival parameters estimated by MARK for the model with the lowest QAIC$_c$. It also includes the standard errors and the 95% confidence intervals for the estimates. I have not given the values determined for the re-sighting parameters as these are not required for the simulation model developed in Chapter 3. They were included in the model analysis so that the best estimates could be obtained for the survival parameters.

Table 2.9. Parameters calculated for the survival equation from the MARK analysis. The parameters are from the best model (Table 2.5) corrected for c-hat=1.08.

Parameter	Beta value	Standard error	95 % Confidence Interval	
			lower	upper
Density dependent parameter (survival)	-0.033	0.007	-0.046	-0.019
Adult age class	4.693	0.230	4.254	5.132
Juvenile age class	4.441	0.427	3.604	5.279
Adult poison effect	-3.687	0.323	-4.321	-3.053
Juvenile poison effect	-1.099	0.623	-2.319	0.122

2.3.14 Environmental stochasticity in survival

I fitted a model that coded each year as a separate variable, but didn't include the density dependent term. The other terms were fitted as described above. This model produced average annual survival rates for adults and juveniles. The expected annual survival (based on the standard model) for each of these years was then subtracted from them. The residual survival probabilities between the two models were used as an estimate of the annual stochasticity in survival. This estimate of environmental stochasticity does not take into account any sampling error, so the estimated value will be higher than the actual variation for the six years of survival data.

Since there were only six years for this analysis, I could not estimate the distribution of the variation. I assumed that it was normally distributed around the mean values calculated by the standard survival model. Calculating the standard deviation of these values gave a result of 0.057 for the juveniles and 0.056 for the adults.

2.3.15 Maximum age/senescence

The oldest recorded age for saddlebacks is 17 years reached by two banded birds on Cuvier Island (Jenkins *et al.*, in prep). However, for two of the comparatively few banded birds to have reached this age implies that the maximum longevity of the species may be considerably longer (Hoyle, 1993). Maximum life span can be calculated by $(\alpha + 4) / (1 - s)$. Where α is the average age of first breeding, and s is the average adult annual survival (Lande, 1988). This gives a value for the maximum age of a saddleback of 45 years (where s is 89%, which is the calculated average annual survival for adult saddleback, and α is one). Age dependent mortality for elderly birds was not fitted in this analysis. Those birds that would have started to show increased mortality rates as a result of age were very few, and would have been among the initial birds released, of which there were 36. Increases in mortality rates in elderly birds are difficult to detect (Botkin and Miller, 1974), without large sample sizes.

2.4 Sex ratio

There was a statistically significant difference in the numbers of males that could be identified compared to the number of females. Of the 122 individuals hatched on the island that were banded and sexed, 50 were female, and 72 were male. The greater proportion of males was consistent over the five cohorts. Therefore, I estimated that any bird being recruited into the population had a 59% chance of being male, and that this would not vary from year to year. The standard error of this estimate was 0.018.

2.5 Discussion

The data for this analysis were collected over five and a half years, so extrapolating beyond this period involved the assumption that the trends seen in this analysis (such as the declines in breeding success and juveniles survival) continue.

2.5.1 Saddleback genetics

I do not consider genetic factors to have much relevance for this project. While genetics is an important consideration for conservation, there is little available information as to the actual effects of inbreeding, or loss of heterozygosity in most species. The population on Mokoia island has expanded quite quickly so there is not likely to have been loss of genetic material within it. Frankham (1995a; 1995b) describes the threats to endangered species from genetic factors such as inbreeding, the accumulation of deleterious alleles, the adaptation to captivity, and the loss of heterozygosity. However, there still remains little empirical information on individual species.

Gilligan *et al.* (1997) found little risk of deleterious mutations being a risk to populations of 25 to 50 individuals for up to 50 generations from population studies of *Dropsophila melanogaster*. One species, for which low levels of heterozygosity have been considered a threat, is the cheetah (O'Brien *et al*, 1985). Whereas its allozyme variation is more homogenous than other species, its mtDNA shows levels of heterozygosity similar to those of other big cat species (Hedrick *et al*, 1996). Caro and Laurenson (1994) offered a cautionary warning about attributing genetic factors to the low density of the cheetah. Their observations identified lion predation of lairs as a major factor influencing high juvenile mortality and low reproductive success. In captivity the low reproductive success was attributed mostly to poor husbandry and maternal neglect. Congenital defects, disease and still births played a lesser role.

To determine the effects of genetic factors on the saddleback population would require an extensive study in its own right to identify the role that was played.

2.5.2 Dispersal

Mokoia is an isolated population with a minimum distance to the mainland of 2.1 kilometres over water. While recently introduced saddlebacks were observed to disperse several kilometres on Kapiti Island (Lovegrove, 1988), this was overland. The saddleback is a poor flyer, and not likely to ever fly 2.1 kilometres over water. Saddlebacks have been recorded to colonise an island over 50m of water, yet there was only one recorded sighting of a saddleback on another island some 200 m further offshore (Newman, 1980).

Juvenile dispersal from the nest was not looked at, but some juveniles dispersed from one end of the population to the other, and the juveniles could access any part of the island. Where they established their territory in the end would depend on whether or not they could compete for a space, or find a free territory.

2.5.3 Age of first breeding

The age of first breeding is a potentially important factor in population regulation (Clobert and Lebreton, 1991). Lovegrove (1980) observed that no first year saddlebacks were breeding on Cuvier Island, a population that had been established for about a decade (introduced in 1968). This matches with predictions from the fecundity and survival analysis that the number of independent fledglings produced declines with population density. From the Mokoia data, first year birds are predicted to produce zero young when the population reaches about 80 pairs.

One question, which I did not have the data to answer, was the effect of old age on reproductive success. It is known that in some species breeding activity decreases in older birds (Dhondt, 1989). This has not been found in saddlebacks to date, although this does not mean that it does not occur. I did find that the reproductive rates of the birds did not decline in birds up to seven years old on Mokoia, but it seems likely that a reasonable proportion of the population will exceed this age from the observed annual adult survival rate (89%) on Mokoia Island.

2.5.4 The pair bond

Saddlebacks mate monogamously, usually for life. There was one observed split on the island while both birds were still alive, so this was considered to occur so rarely that it would have a negligible effect on the population. Usually the pair bond was ended when the one of the birds died.

2.5.5 Pair quality

This term includes a number of different factors, which could not be isolated for their individual effects. These include the quality of the male, the quality of the female and the quality of the territory.

Pair quality has been modelled as a variable explaining variation between individuals in their reproductive success. In reality better quality pairs might start breeding earlier than others or have heavier chicks and fledglings (Colby *et al.*, 1998), or a larger clutch size (Coulson, 1985).

2.5.6 Use of nest boxes

Another potential factor affecting observed pair quality was the use of nest boxes. There were a large number of nest boxes on Mokoia, and there was always at least two per pair. However, box use varied among birds, with some birds using boxes consistently, some not using them at all, and most birds used boxes sometimes and natural cavities other times. While saddlebacks are classified as cavity breeders, they will use a wide variety of protected sites for breeding.

The use of nest boxes can lead to the overestimation of fledgling success (Clobert and Lebreton 1991), because the nest boxes can provide better nesting sites. Lovegrove (1992) found no difference in the clutch sizes laid by saddlebacks using natural or artificial cavities on Kapiti Island. Variations in the use of nest boxes with different age classes also have the potential to produce misleading estimates of the mean age of the breeders (Clobert and Lebreton, 1991). Variations in nest box size have also been found to affect clutch size in some species (Gustafsson and Nilsson, 1985; Moeed and Dawson, 1979), with the size of the clutch being adjusted to the size of the nest box/cavity being used (Karlsson and Nilsson, 1977).

Because saddlebacks on Mokoia used both nest boxes and natural cavities, it was not possible to do a simple comparison of box users and non-box users. However, we calculated two indexes of box use (see Section 2.2.3). There was no correlation between these and the measure of pair quality, suggesting that nest boxes did not affect reproductive success during the years studied. It is possible that nest sites will become more limiting as population size increases. However, my simulation modelling in Chapter 3, suggests that the population will not increase substantially beyond the level it had reached at the end of this study.

2.5.7 Density dependent effects

The concept of density dependent population regulation is deduced through a logical deduction from one major premise, the persistence of populations (Royama, 1977). If a population's size were not regulated in some way then it could potentially keep on expanding. Density dependent effects are factors that are correlated with the size/ density of the population, although an explanation based on population density/size for population regulation is not an explanation, as population density is a derived relationship (Turchin, 1999).

Density dependence has been found through empirical and simulation studies to be difficult to detect in natural populations because of the confounding influences of environmental and demographic stochasticity (Royama, 1977; Lebreton, 1990; Burgman *et al.*, 1993). However, in the Mokoia Island population, there were clear declines in juvenile survival and reproductive success, correlating with the increased population density. Because this was a reintroduced population we had the advantage of being able to obtain data at a range of densities without density being confounded by environmental conditions. The question remains as to what regulated the Mokoia Island saddleback population. Density dependent reproductive success and juvenile survival, with density independent adult survival, has been found in other passerine species (Blue tit: Dhondt *et al.*, 1990; song sparrow: Arcese *et al.*, *1992*).

Andrewartha and Birch (1954) emphasised the non-uniformity of the areas where populations live. As population size increases, more individuals are forced into poor quality territories and the reproductive success of these individuals is influenced by the quality of the territory. This is density dependent fecundity. As the population size increases, proportionally more poor quality sites are occupied (Dhondt *et al*, 1992). The population's rate of growth does not reduce, because the reproductive success decreases in all territories. It decreases because proportionately more birds have smaller clutches, as the proportion of occupied poor quality sites increases. This will occur where habitat heterogeneity occurs at the level of the individual territories.

The density dependent effects on Mokoia Island could have been caused by the restriction of access to resources, or territory, yet O'Callaghan (1980) estimated the average territory, as 0.45 hectare on Cuvier Island. Assuming that the saddlebacks on Mokoia have similar sized territories then the expected carrying capacity of the island would be 300 pairs. This is a simple extrapolation ignoring any effects for differences of habitat. Lovegrove (1992) estimates a carrying capacity for the island of 500 birds, based only on the size of the island, and estimated population densities on other islands (although the methods used for these estimates were weak, and their accuracy must be questioned).

A by-product of population regulation by territorial behaviour is the occurrence of floaters (Brown, 1969; Smith and Arcese, 1989). Floaters are reproductively capable adults that are socially excluded from breeding by territory saturation. Ens *et al.* (1992) and Zack and Stutchbury (1992) suggest that floating is an alternative strategy to breeding immediately. There may be a choice between occupying a poor quality territory now, that will be retained by that individual for the rest of its life, and floating with the possibility of obtaining a better territory later (Kokko and Sutherland, 1998). Floaters may have decreased reproductive success (Smith and Arcese, 1989), and may also have a higher mortality (Arcese, 1989; Smith and Arcese, 1989; Brown, 1969). Although no birds were observed to remain unpaired beyond their first year on Mokoia Island, the population was expanding. On Tiritiri Matangi Island, where there is an established saddleback population, floaters have been recorded remaining unsettled for more than one year (Hoyle, 1993). This is also the case on Mokoia Island where the majority of unpaired males seem to establish a territory.

2.5.8 Sex ratio

The sex ratio of the saddlebacks surviving to breeding age was strongly male biased. This raises some interesting questions as to the cause of this and whether it will continue. As the saddlebacks were difficult to sex until they were about one year of age, it is unknown whether this results from a skewed sex ratio or in different survival rates within their first year. Determining this would require developing of sex specific DNA markers so that hatchlings can be sexed in the nest.

2.6 Summary

The analysis in this chapter has identified properties of the saddleback population on Mokoia Island that are needed to successfully model it. These properties are:

- Reproductive success, and the terms that effect this:
  - Pair quality.
  - Male age class (1st year older birds).
  - Female age class (1st year or older birds).
  - Population density (measured as number of pairs at the start of the season).
- Survival, and the terms that predict this:
  - Age class (adult or juvenile).
  - Population density (on juvenile survival only).
  - The effect of the poison drop.
- Sex ratio of birds recruited into the population.

3

The Model

3.0 Abstract

I constructed a model of the Mokoia Island saddleback population using the demographic parameters calculated in Chapter 2. This model predicted that the population would fluctuate around an average population size of 103 pairs, with 44 unpaired males. Due to the male bias in the sex ratio of birds reaching adulthood, there were no unpaired females. The estimated value of the population's growth rate for the first four years was 1.62. The estimates of the average number of pairs each year closely match the observed data set.

I performed a sensitivity analysis on the model to identify those parameters with the most influence on the model's output, within their range of uncertainty. This was determined by comparing changes in the average population size at the end of 50 years, and the average growth rate over the first four years, when the parameter estimates were set at the extremes of their 95% confidence intervals. The parameters with the most negative effects on population size (with the parameters at -1.96 standard errors from their estimated values) were: the density dependent parameter for juvenile survival (population reduced to 75 pairs), and the juvenile survival intercept (population reduced to 77 pairs). The density dependent parameter in juvenile survival caused the greatest increase in population size at +1.96 standard errors (population increased to 161 pairs). The parameter that had the most negative effect on growth rate in the first four years (at -1.96 standard errors) was the juvenile survival intercept (growth rate reduced to 1.49). The parameters that produced the greatest increase in growth rate were: the density dependent parameter in juvenile survival (growth rate increased to 1.73), the intercept value for adult survival (growth rate increased to 1.74), and the intercept value for juvenile survival (growth rate increased to 1.72).

The average population size was influenced by the method used to incorporate environmental stochasticity. Using the estimates of environmental stochasticity obtained in Chapter 2, the model produced an estimate of 103 pairs, whereas using the standard errors for parameter estimates produced higher average population sizes.

3.1 Introduction

In this chapter I construct a model of the Mokoia Island saddleback population using the demographic parameters determined in the previous chapter. My first goal was to create a model that would mimic the population growth recorded on Mokoia Island. This model was then used to estimate how large the average population size will be (as the model includes environmental stochasticity, the population size will fluctuate from year to year). It was also used estimate how many years the population will take to reach this level and to establish the viability of the population. Once the model had been constructed I performed a sensitivity analysis to identify those parameter estimates that are likely to have the most impact on the population, when sampling uncertainty is taken into account.

3.1.1 Modelling

A model is a representation or abstraction of a system or process. Building models allows us to: (1) define problems, (2) understand data, (3) make predictions (Starfield and Bleloch, 1986).

Models can provide understanding of what determines the extinction or persistence of small populations and then simulate the consequences of various management options to identify the cheapest and/or most effective means to conserve populations (Hamilton and Moller, 1995). A model can be used to help determine what data need to be collected.

It is impossible to create a completely realistic model, except for extremely simple systems. However, this is not the role of modelling. The role of modelling is to explore rigorously the effects of certain assumptions made about a system. The predictions of models should not be used as a substitute for field experimentation, but as an aid for its planning (McCallum, 1994). If used successfully they enable the fieldwork to be focused more accurately on critical questions. The goal of the modeller is to identify the important variables in the system that explain the majority of the variation.

There are two ways of considering models (Starfield, 1997). We can treat them as an approximation to the "truth", or we can treat them as a problem-solving tool. The model created in this chapter is an approximation of the saddleback population on Mokoia Island, but it will also be used as a problem-solving tool (Chapter 4). In that chapter I will look at possibilities for population management for the saddleback, including possible harvesting strategies for the Mokoia population, and the possibility of a poisoning program allowing saddlebacks to be reintroduced onto the mainland.

The quality of the information used to construct the model is important. The results are only as good as the data that is used to create the model and the assumptions that were made during its construction (garbage in, garbage out). If the wrong information is used, or the assumptions are mistaken, then spurious results will be produced, which may prove detrimental to the species in question (Brook *et al.*, 1997).

Models can be divided into two groups: deterministic and stochastic. Deterministic models do not include any random variables so there is no element of uncertainty. Stochastic models include random variables. Natural populations live in uncertain environments, and it is now generally acknowledged that stochastic models are needed to simulate their dynamics (Starfield and Bleloch, 1986; Burgman *et al.*, 1993).

Environmental stochasticity is a major factor affecting populations (Caughley & Gunn, 1996). Including environmental stochasticity decreases the viability of populations (Shaffer, 1981). Goodman (1987) showed that including environmental fluctuations in a model can lead to large decreases in persistence times when compared with models that only consider random differences between individuals. Environmental stochasticity is generally modelled as white noise, where any two points in time are un-correlated (Ginzburg *et al.*, 1982). The assumption that environmental stochasticity is not autocorrelated may provide an adequate approximation, because regional weather conditions have low autocorrelation on time scales of a year or longer (Lande, 1987).

The dynamics of small populations are governed by the fortunes of each of its few individuals, whereas the dynamics of large populations are governed by the law of averages (Caughley, 1994). For this reason, demographic stochasticity (stochasticity that acts at the level of the individual) has been included in this model.

There is little point in examining a single run of a stochastic model (McCallum, 1994). The inclusion of random variables means that each run of the model will differ from the last, at least to some degree. By running many simulations it is possible to estimate a probability distribution for the possible outcomes. It is also important to remember that reality is only a single run of a highly complex model. There will always be discrepancies between our predictions and reality.

3.1.2 Population Viability Analysis

Population viability analysis (PVA) is an important tool for risk assessment of endangered species (Boyce, 1992; Possingham *et al.*, 1993; Possingham *et al.*, 1994; Ruggiero *et al.*, 1994; Armstrong and McLean, 1995). It is an application of modelling to the management of threatened species. PVA can guide conservation management and research by predicting the cheapest and most effective actions required to conserve populations (Hamilton and Moller; 1995). PVA can be used to guide research programs, develop conservation strategies, and to inform decision and policy making for both endangered and non endangered species (Lindenmayer *et al.*, 1993). It is a useful management tool for allowing predictions of the factors that are important for the continued survival of a population.

Modern conservation biology focuses on managing small populations, and this requires estimating their viability (or vulnerability to extinction) so that any appropriate management action can be taken (Lindenmayer *et al.*, 1993). Shaffer (1981) introduced the idea of a minimum viable population (MVP) size for management of endangered species. His nominal definition of a MVP was the smallest population with a 0.99 probability of surviving for 1000 years. However, there is no single answer to the problem of what the minimum viable population size is for a species. It depends on the biology of the species, and on the options that are available regarding the size, number and location of suitable habitat patches that can be preserved (Nunney and Campbell, 1993). In reality the MVP concept is a convenient management term. Populations become more vulnerable to extinction the smaller they become, and minimum sizes are calculated from arbitrary criteria given by managers.

There are a variety of PVA software programs. Some of the more commonly used programs are: ALEX (Possingham and Davies, 1995), VORTEX (Lacy, 1993), RAMAS/metapop (Akçakaya, 1996) (see Lindenmayer *et al.*, 1995 for a comparison of these three), INMAT, and GAPPS (Brook *et al.*, 1997). The use of even simple computer models for PVA can provide more accurate predictions about population dynamics than the more crude techniques available previously, such as calculation of expected population growth rates from life table data (Lacy, 1993).

I constructed a purpose built model for the PVA of the Mokoia Island saddleback population, rather than use a prefabricated program such as ALEX or VORTEX. Existing software packages have the advantage that they have already been extensively tested, and models can be produced quickly and easily. However, a purpose built model can be tailored to suit a particular purpose, and to fit the characteristics of the system. The assumptions that it is built around will be based on the particular species in question, and specific behavioural traits can be included if they are likely to affect the population (e.g. Vucetich *et al.*, 1997). A purpose built model allows the inclusion of specific events, such as the poison drop, which occurred in September of 1996. A detailed model like VORTEX is more appropriate to use when you have detailed information on the behaviour and fates of individuals over a short period of time. Vortex does not allow age specific reproduction, density dependent effects on mortality, or stochasticity in reproduction (except for the proportion having greater then zero offspring). In addition, it is useful for biologists to learn to build their own models (with or without software) rather than having fieldwork and modelling carried out by different sets of professionals (Akçakaya and Burgman, 1995).

3.1.3 Individual-Based Modelling

One of the problems when models are applied to field research and experimentation in ecology is that reality is complex. Whereas mathematical modelling in ecology requires simplifying assumptions, some of these are not compatible with the reality of ecological systems. One of the most important of these assumptions is that individual members of populations can be aggregated into a single variable represented as population size. Many classical models in ecology, such as the Lotka-Voltera equations, assume that all individuals in a population are identical and that all are affected equally by events (DeAngelis and Gross 1992). This is obviously not the case, and while it may be practical to assume all individuals are identical when studying the behaviour of large populations, this is not the case for small populations. The essence of the individual based approach is deriving the properties of ecological systems from the properties of the individuals constituting these systems (Lomnicki, 1992; Hasswell and May, 1985). For example, models that do not distinguish between individuals will tend to predict the population's extinction at low resource levels. In reality, those dominant individuals will exclude the less fit from the resource, and the population will survive for longer periods than predicted (Lomnicki, 1988).

Different types of models are appropriate for different situations. A population-level model can be used for broad patch occupancy data, which does not have information on the individual populations (such as many models used in metapopulation theory e.g. Levins, 1969; Hanski and Simberloff, 1997). When we have detailed information on individuals, the best way to model this is with an individual based model.

Individual based modelling is a relatively new approach, only recently becoming a useful tool as personal computers became more powerful and accessible (Huston *et al.*, 1988). Individual based models allow individuals to be kept track of, and the interactions between them to be simulated. Individual based modelling represents one extreme of the population-modelling continuum (Uchmañski and Grimm, 1996). At the other extreme are models based on the average individual (e.g. logistic growth), where individual variation is ignored. In the middle are those models that are stage structured, keeping track of the number of individuals of each age class and sex, but still based on the average individual (e.g. ALEX, VORTEX, and RAMAS; Lindenmayer *et al.*, 1995).

Each bird is stored as a unique individual within my program and I have attempted to include some individual information. Each pair is considered to be a separate entity with a unique value for pair quality, which is used in the reproduction equation.

3.2 Model structure

I constructed the model using the computer programming language C++. C++ is an object-orientated language, allowing me to break the program down into functions to complete specific tasks, such as reproduction and mortality. The program was compiled using Borland C++ 4.5.

Paired and unpaired adult birds are stored in arrays within the model. These arrays store the ages of the birds and a value for the quality of each pair. Juveniles are not treated as individuals and one variable is used to store the number of juveniles. There was no need to store the juveniles in an array as they are of unknown sex until they reach breeding age.

3.2.1 Sequence of program flow

"Fledgling" describes birds just created by the reproduction function. "Juvenile" describes birds in their first year, and "adult" describes birds older than one year.

The flow of the program is as follows:

(1) The random number generator is seeded.

(2) The arrays used to store paired and unpaired birds are initialised.

(3) The initial population is created. For the sensitivity analysis this consisted of fifteen pairs with each bird having a randomly determined age between the years one and five years (inclusive). For the comparison with the actual data, the initial population consisted of 20 males and 16 females with randomly determined ages between one and five. These birds were not paired, and were subjected to 6 months mortality before the first breeding season.

(4) The value for the amount of environmental stochasticity for that particular year is randomly determined (Section 3.2.7). This value is then used to add environmental stochasticity to: reproduction, juvenile survival, and adult survival.

(5) The reproduction function is called which calculates the number of independent fledglings produced for each pair in the population, rounded to the nearest whole number. This number is determined by the ages of the male and the female, pair quality, population density, the value determined for environmental stochasticity for that year (see Section 3.2.6), and a random element determined for each pair.

(6) The adult survival function is called on the arrays containing paired males, paired females, unpaired males, and unpaired females. This function calculates the

probability of each bird surviving the next 12 months. This value remains relatively constant with the only variation being due to environmental stochasticity (see Section 3.2.5). The function produced a random number between 0 and 1 (from a uniform distribution) for each bird in the array. If this number is greater than the survival probability then that bird is dead, and its age is reset to zero. All birds reaching 30 years are also killed.

(7) The juvenile survival function is called on the variable used to store the number of fledglings. The survival probability of a bird in its first year is calculated based on the density of the population (see Section 3.2.5). The function then produces a random number between 0 and 1 for each juvenile as described above for adults. If this number is higher than the survival probability then the term storing the number of dead birds is incremented by one. The variable storing the number of juveniles is then reduced by the number of birds that died.

(8) The arrays are then reorganised so that all birds are stored together within the array, rather than with zero values between them. Those birds that have lost partners are moved into the arrays that store the unpaired individuals.

(9) The ages of all adult birds are incremented by one year.

(10) Juveniles are assigned a sex and placed in the appropriate array for unpaired birds. Sex is assigned by producing a random number from a uniform distribution between 0 and 1. If the number is higher than the observed sex ratio (see Section 3.2.3) then the bird is placed in the array for unpaired males. If the number is equal to or less than this number, it is placed in the array for unpaired females. When they are placed in the unpaired arrays, they are given an age of one.

(11) New pairs are formed. The program determines which of the unpaired arrays (male or female) has the lesser number of birds in it. It then gives all these birds a partner from the opposite sex. These are then moved to paired arrays and are assigned a randomly determined value for pair quality.

(12) The population is tested to see if it is extinct. The population is considered to be extinct when there are zero birds of either sex.

(13) After each 50-year run the final number of birds is stored.

(14) The arrays used to store individuals and pair quality are reset to zero values (after other simulation runs).

(15) Steps 4 to 14 are repeated to simulate the population over 50 years.

(16) Steps 3 to 15 are repeated 1000 times to provide replicates of the population's

performance.

(17) Once all simulations have been completed the model calls the statistics function. This calculates the average and standard deviation for the number of pairs and number of unpaired birds of both sexes in the last year of the simulation.

This is the sequence that all versions of the program followed. There were some alterations made to the program so that different results could be obtained from it. To obtain values for the growth rate, the program was altered so that the numbers of pairs in the population over the first four years were stored. However this increased the amount of memory that the program used, so the number of simulations was reduced to 200.

3.2.2 Calculation of the population's growth rate

The growth rate was calculated for the first four years, then these values were pooled for all simulations and the average and standard deviation calculated. The equation used to calculate the growth rate was exponential growth in discrete time:

$$N_{t+1} = rN_t.$$

This simple model does not include any form of density dependence, but is suitable for a comparison of the effects of parameter changes as it is only applied to the first four years. I attempted to fit the discrete time, density dependent equation, as this equation models a decline in growth rate as the population expands:

$$N_{t+1} = N_t[1 + r(1 - N_t/K)]$$

This was applied to each of the first four years, and K was set to 103. However, the growth rate did not remain constant over the four years for which it was measured. Therefore, I decided to use the simpler equation above. The reason that the growth rate did not remain constant using the discrete time exponential model with density dependence was that the density dependent relationship in my model is more complex than the simple linear decline modelled by the logistic model. While the decline in reproductive success is modelled as a linear trend, the effect of population density on juvenile survival is not linear, as the parameter is logit transformed to produce the survival estimate (see Section 2.3.2 and Figure 3.1).

3.2.3 Assigning sex

Juveniles were not accurately sexed until their first breeding season, so there were no data on the primary sex ratio or separate juvenile mortality rates for males and females. Juveniles were assigned to a sex after they had survived their first year. The sex ratio was 0.69 females to 1 male, based on the observed sex ratio on Mokoia Island over the five years. This ratio did not appear to change over time so I have assumed that it was not affected by population density.

3.2.4 Dispersal

Dispersal was not included in this model. Mokoia is an isolated population, and juveniles can easily disperse to any point on the island. The model is not spatially explicit, so no dispersal away from the population was modelled, nor was dispersal away from the nest for fledglings.

3.2.5 Survival

The parameters that were calculated in Chapter 2 give the probability of a bird surviving for one month. To extend this to one year the values needed to be raised to the power of twelve. However birds were considered to be juveniles for nine months. Therefore, their expected survival over their first year was calculated by raising juvenile monthly survival to the power of nine, then multiplying this value by the adult monthly survival raised to the power of three. Juvenile survival for one month is calculated by:

$$\frac{e^{(\beta_1 + \beta_2)}}{1 + e^{(\beta_1 + \beta_2)}}$$

β_1 is the intercept value determined for juvenile survival using (Section 2.3.11) is 4.44. β_2 is the density dependent parameter, which is -0.003 multiplied by the number of pairs breeding that season. The expected annual survival for birds in their first year (including both adult and juvenile components) is 87.5% with zero pairs. This declines as the number of pairs increases, and reaches zero at approximately 130 pairs (Figure 3.1).

Adult survival for one month is calculated by:

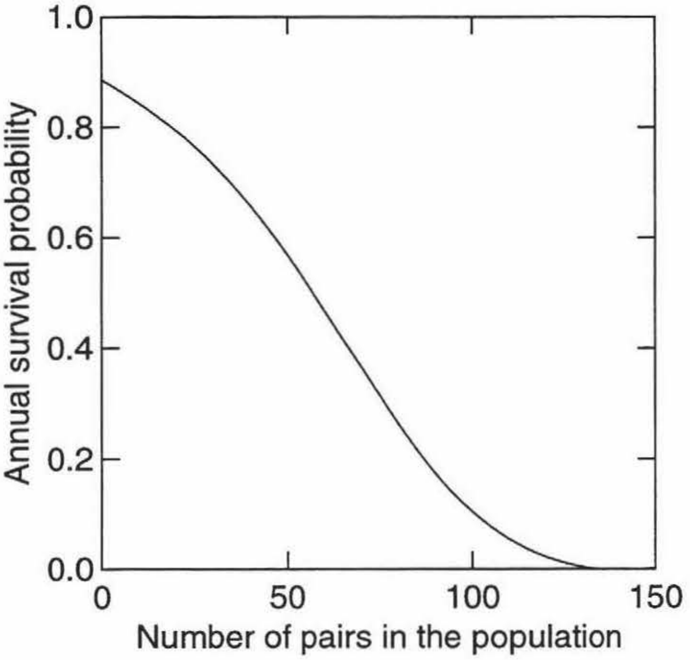
$$\frac{e^{(\beta_3)}}{1 + e^{(\beta_3)}}$$

Where β_3 is the value for the adult survival intercept which was determined using MARK to be 4.69. The expected adult survival probability is 89.5%. The actual survival probability for both adult and juvenile birds are then adjusted according to the value for environmental stochasticity for that year (see Section 3.2.7).

3.2.6 Reproduction

All pairs alive at the end of the year could potentially have produced independent fledglings. These pairs are subjected to the reproduction function, where it is possible that no fledglings are produced. The equation used to simulate reproduction was determined in Chapter 2. It was implemented for each pair in the population during

Figure 3.1. Decrease in annual juvenile survival probability as the number of pairs in the population increases. The curve is calculated using the juvenile survival equation determined in Chapter 2.



each "breeding season" to determine the number of independent fledglings would be raised by that pair.

The equation used is:

> Intercept + male age class + female age class + pair quality + density dependent value + random number.

The intercept had a value of 3.2. Male and females both have two classes. First year males had a value of -0.35, second year and older males had a value of 0.35, first year females had a value of -1.0, and second year and older females had a value of 1.0. Pair quality is the value determined for each pair, and it has a mean of zero and standard deviation of 1.26. The density dependent value is -0.017 times the number of pairs on the island. The random number is produced from a standard distribution with a mean of zero and a standard deviation of 0.77. This value was obtained by examining the residuals when the general linear model was fitted to the reproductive data (see Section 2.2.8).

3.2.8 Stochasticity

This model includes two kinds of stochasticity, demographic and environmental. Demographic stochasticity is the variation in fortunes between individuals. Some animals live, while others die, some become male while others are female, and some pairs are better than others. Environmental stochasticity is variation due to outside causes such as weather, which influence the population as a whole.

Demographic stochasticity was incorporated into the model in several places. It was in the survival functions, the function for assigning sex, the function for creating new pairs, and the reproductive function. It occurs in the survival equations, as the random number that is produced for each individual, to work out if it lives or dies. It occurs in the function for creating pairs, as the random value assigned to each pair as a measure of its quality. It occurs in the function for assigning sex, as the random number used to determine the sex of each bird. It occurs in the reproductive equation, as the random number that is added to each pair's reproductive output.

Environmental stochasticity is incorporated into this model in three places: in the values for reproductive success, juvenile survival, and adult survival. It was simulated by producing a random number from a normal distribution with a mean of zero and a standard deviation of one. This was the general value for environmental stochasticity for that particular year. I assumed that the stochasticity in survival and reproduction would be concordant, i.e. a good year for reproduction would be a good year for survival of both adults and juveniles. To convert the general value for environmental stochasticity into values for each function, the general value was multiplied by the standard deviations of the terms for environmental stochasticity of each function (adult survival, juvenile survival, and reproduction), which were calculated in Chapter 2. This produced three specific values that were then used in their respective functions.

The values for environmental stochasticity in survival were added to the expected survival probabilities for adults and juveniles (Section 3.2.5). The value for environmental stochasticity for reproduction was added to the number of fledglings produced for each female. As the environmental stochasticity for all three functions was from a normal distribution with a mean of zero, it could also be either negative or positive from year to year. The standard deviation for adult survival is 0.057, for juvenile survival it is 0.056, and for reproduction is 0.202.

3.2.8 Assumptions of the model

There are some key assumptions made in the model. I discuss each of these in turn.

1) *All birds will form pairs if there are enough members of the opposite sex*

Hoyle (1993) records that not all birds pair immediately after the loss of their mate. However, on Mokoia there was always an excess of males, and all females were paired in every breeding season. This does not rule out the possibility that some females may have remained unpaired, but this was never observed in five years on Mokoia Island, so it must occur so infrequently that it will be unimportant to the population.

2) *Individual variation is not heritable*

This model takes into account some individual variation, in the form of pair quality, but this is not passed down to surviving offspring. It is possible that good quality birds pass on these good characteristics to their offspring. However, I am assuming that reproductive success will not improve over time due to natural selection. Unless this occurs, inheritability of individual variation is irrelevant to the model since genetic factors are not included.

3) *The effect of density on parameters will remain constant*

It is possible that the capacity of Mokoia Island to support saddlebacks will change over time as the forest matures, as the island currently consists mainly of relatively young re-growth.

4) *Pairs remain together until one-member dies*

There was only one case of "divorce" observed on Mokoia among 81 pairs recorded. This was deemed to occur so rarely among the pairs followed as to be unimportant to the population.

5) *The island is not subject to catastrophes*

Truly major catastrophes seem so idiosyncratic that it is hard to imagine a predictive model for their occurrence and effect (Simberloff, 1988). If catastrophes are relatively rare on a human time scale, then a model will only be useful for management once the catastrophe has occurred and the effect on demographic parameters is known (Hoyle, 1993). There is no reason to expect extreme years to occur on a regular basis, such as those due to fires or El Niño in some systems.

6) *All birds attempt to breed at the same time, and die at the same time*

The population processes are considered to occur at the same time for all birds. This is not so much an assumption as a simplification for modelling convenience. To produce a model that simulated the population on a day to day level would require more computer resources than are readily available, and would take a much longer time to complete. In reality, mortality can occur at any time of year, and the breeding season of the species on Mokoia Island can extend over half a year (with the first eggs laid as early as September and the last young fledgling as late as April).

An effect of this assumption is that the model doesn't explicitly consider the reduction in breeding success due to mortality of either the male or female during the breeding season. However, this is accounted for in the reproductive rates used in the model, which were based on the number of females alive at the start of the breeding season.

7) *Environmental stochasticity that results in a good year for survival will also result in a good year for breeding*

I decided that it is unlikely that a bad year for survival would correspond to a good year for reproduction, or for the opposite to occur. I considered that any conditions that would increase adult survival would be likely to increase juvenile survival and reproduction on the island.

8) *No negative fledglings can be produced*

The equation that describes the reproductive data creates the possibility of negative fledglings being produced by a pair. However, within the reproductive function in my model, any negative fledglings produced by a pair were treated as zero fledglings, and the reproductive output for each pair was rounded to the nearest whole number at the level of the pair. In fitting a linear model to the data, a normal distribution for the number of fledglings produced was assumed. This is not the case, as in reality a pair cannot have less than zero fledglings, whereas the fitted model predicts this under certain circumstances (high population density, very poor pair quality).

3.3 Sensitivity Analysis

Decisions are often made with missing data, and this is where modelling is useful. Also, the parameters that are estimated are subject to error, so there is some uncertainty in results obtained from the model (McCarthy, 1996; Drechsler, 1998). A sensitivity analysis can be used to assess the effect of this on the models output, as well as testing the effect of the assumptions that were made as the model was constructed.

This sensitivity analysis is broken down into two related parts, structural sensitivity analysis and parameter sensitivity analysis. For conducting the sensitivity analysis the population started with 15 pairs and no unpaired birds. All birds were given a randomly determined age between 1 and 5, with equal probabilities for each age.

Two measures were used to assess the impact of changes to the model on the population. The first measure was the number of pairs at the end of the 50-year period for which the model was run. The second was the average growth rate for the first four years (the calculation of this is discussed under Section 3.2.2). The calculation of the population's growth rate is based on 200 simulations, and the calculation of the average population size is based on 1000 simulations.

3.3.1 Structural sensitivity analysis

Structural sensitivity analysis involves removing or replacing elements of the structure of a model, then examining changes in the outputs. The purpose is to determine which elements of the model are important and which are not (Hoyle, 1993).

Five structural changes were made. (1) The order in which the reproduction and survival functions were called was reversed. (2) Environmental stochasticity was removed from the program (this is the "model without environmental stochasticity" in Table 3.2). (3) The way in which environmental stochasticity is included was altered, so that the environmental stochasticity in the survival and reproduction functions was not concordant. Values for environmental stochasticity were determined separately for reproduction, adult survival, and juvenile survival. This is "model with environmental stochasticity unlinked" in Table 3.2. (4) The way in which environmental stochasticity was estimated was altered. Adult survival was altered so that it was based on the standard error for the intercept term for the adult age class (see Table 2.9 for parameter estimates). Juvenile survival was altered so that environmental stochasticity was based on the standard error for the juvenile age class intercept (see Table 2.9 for parameter estimates). Reproduction was altered so that the environmental stochasticity was based on the standard error for the intercept term fitted in the analysis (see Table 2.3 for parameter estimates). This was named "model with altered environmental stochasticity". (5) The reproductive equation was altered so that a pair could produce negative fledglings, and so that the rounding of the number of fledglings produced per pair occurred at the level of the population, rather than at the level of the pairs. This is "model with altered reproductive function".

3.3.2 Parameter sensitivity analysis

Assessing the model's sensitivity to changes in parameter values is useful for two reasons. Firstly, if sensitive parameters can be changed through management intervention, such as supplementary feeding or predator control, then it may be possible to influence the dynamics of the population in a desired direction. Secondly, there is always error in the data used to define parameters for a population model, and uncertainty in parameter estimates can effect the strength of the conclusions reached. By varying parameters over a range of uncertainty (e.g. 95% confidence interval), we can determine if uncertainty in any parameter affects the model's output. These parameters can then be researched more thoroughly, and more accurate estimates obtained (Lindenmayer *et al.*, 1993).

To perform the sensitivity analysis I altered the values of the main variables in the model. These were the coefficients and constants determined for reproduction and mortality of the Mokoia Island population. I varied the parameters by 1.96 standard errors on either side of their estimated value so that the effects on the edge of the 95% confidence interval could be seen. I also varied the parameters by up to three standard errors either side of the estimate and these results are shown in Appendix C.

The parameters altered from the reproduction equation were:

the intercept determined from the regression equation,

the effect of male age class,

the effect of female age class,

the effect of the density dependent coefficient.

The parameters altered from the survival equation were:

the effect of adult age class,

the effect of juvenile age class,

the effect of the density dependent coefficient.

The variables that were altered in combination were:

both density dependent coefficients (reproduction and survival),

both intercepts in the survival equations (adult and juvenile).

I also examined the effect of maximum age, and the size of the standard deviation for pair quality. There were no estimates of the standard error for these parameters so I used different schemes to vary them. Maximum age was examined by looking at the effects on population size of the two values that it was predicted to lie between, 17 years (oldest recorded ages, Jenkins *et al.*, in prep) and 45 years (the predicted maximum life span, estimated in Section 2.3.18), as well as a range of values between this.

To see the effect of pair quality on the model, I ran a series of simulations where the value for the standard deviation of the parameter was multiplied by zero and up to five. This alters the standard deviation for pair quality from 0 (when multiplied by zero) and up to 6.3 (when the parameter was multiplied by five).

In addition to varying the parameter estimates to the extremes of their individual 95% confidence intervals, I computed the average number of pairs where the parameter in question was varied by up to three standard errors from the estimated value in both directions.

Table 3.3 gives the results of the sensitivity analysis where the parameters are varied by +/- 1.96 standard errors, which gives a 95% confidence interval for the parameter. I was concerned with the uncertainty in the estimates of the parameters (hence the use of the standard errors) rather than with the actual distribution of the data (for which standard deviations would have been used).

3.4 Model results

The population always increased for about six years after 15 pairs were introduced and then the average population size remained at about 103 pairs (Figure 3.2, Table 3.1). The population expands rapidly after release, until it reaches a point where reproduction balances mortality (Figure 3.2). The population then fluctuates around this level through stochasticity (Figure 3.3), with individual populations typically varying between about 80-140 pairs over time (Figure 3.3). When the population began with the same number of birds as were released on Mokoia, it closely followed the recorded increase in the number of pairs (Figure 3.4). The number of pairs on Mokoia Island in the 1996-97 breeding season is omitted from Figure 3.4 because a poison drop occurred before that breeding season. This reduced the number of pairs to almost exactly the same number as in 1995-96, hence 1997-98 is considered to represent the fifth year. At this stage the model does not include the poison drop (this will be included in Chapter

Figure 3.2. Average number of pairs in the population over 50 years after release, from 100 simulations. The error bars represent one standard error from the mean. The initial starting population size was 15 pairs.

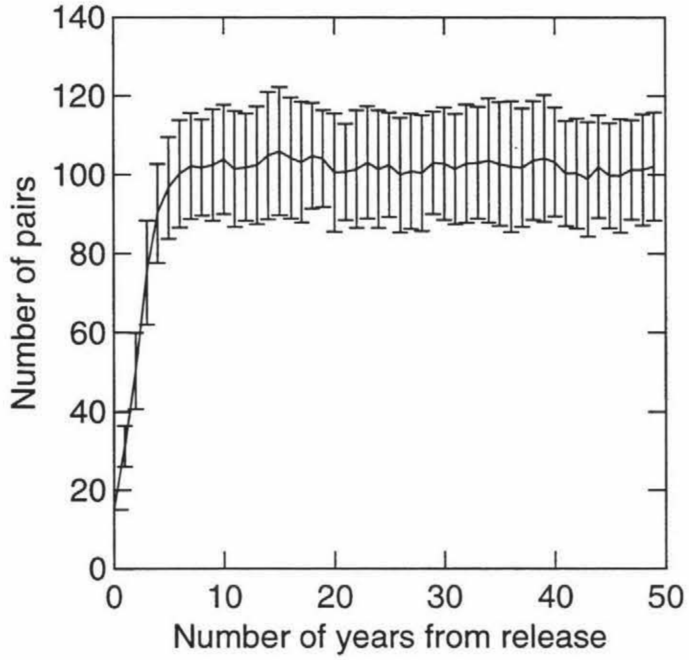


Figure 3.3. Variation in the number of pairs over time from one run of the model. The initial population size was 15. The population can be seen to vary between 76 and 140 pairs, after the initial increase from the starting population.

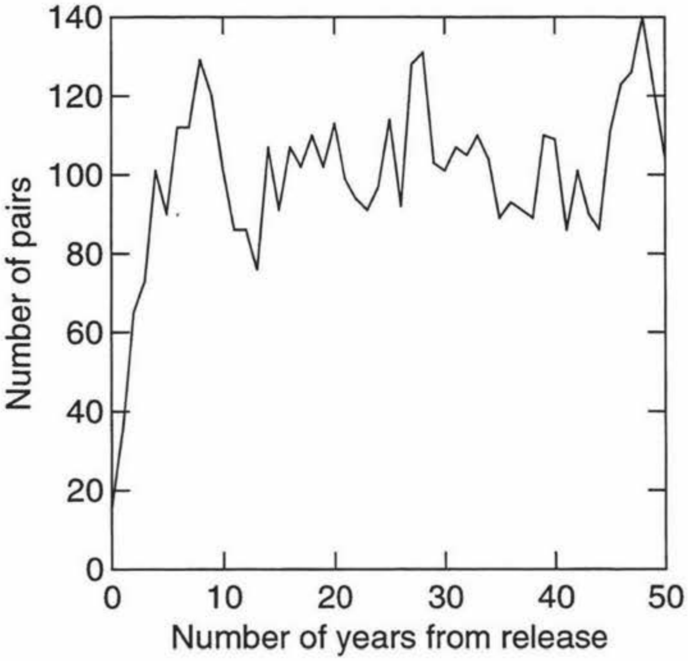
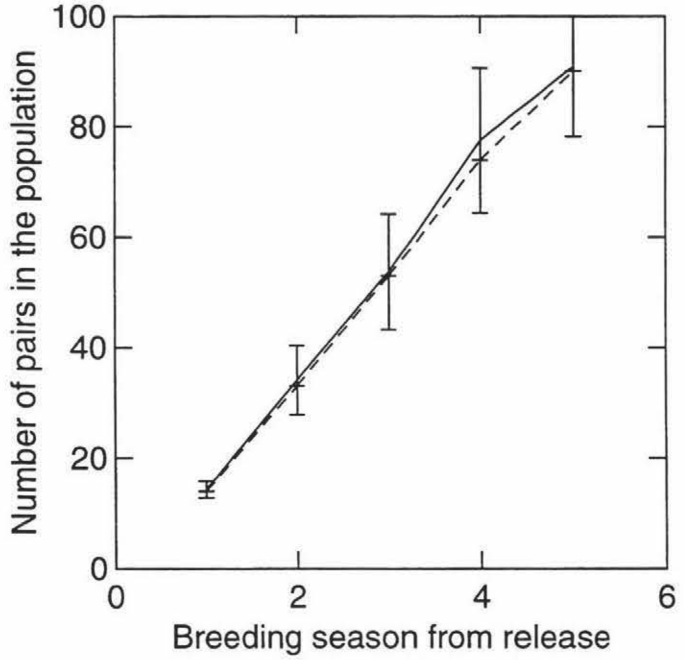


Figure 3.4. Comparison between the simulated number of pairs and the recorded number of pairs from the Mokoia Island saddleback population. Breeding season 1 corresponds to the 1992-93 breeding season, 2 is the 1993-94 breeding season, 3 is the 1994-95 breeding season, 4 is the 1995-96 breeding season, and 5 is the 1997-98 breeding season. The 1996-97 breeding season is omitted because of a poison drop, immediately before it (see text for details). The error bars represent one standard deviation from the mean.



4).

The population's viability is good. The only conditions under which the population went extinct was when the parameters for density dependence in reproduction, density dependence in survival, adult survival intercept, juvenile survival intercept, and the reproduction intercept were varied by minus 4 standard errors simultaneously. This is unlikely to be realistic, as the chances of these five parameters being overestimated by 4 standard errors each is extremely low.

Table 3.1. Results from saddleback model without poison. Values show means with 95% confidence intervals. Values for the average number of pairs and the average numbers of unpaired males and females are from the 50th year, produced from 1000 simulations. The values for growth rate are the average value for the first four years, taken from 200 simulations

Number of pairs	103 +/- 1
Numbers of unpaired males	44 +/- 1
Number of unpaired females	0 +/- 0.
Growth rate	1.62 +/-0.05

3.4.1 Results from structural sensitivity analysis

(1) Model with program sequence altered (Table 3.2)

This produced no significant difference in the average size of the population. However the population's growth rate was increased from 1.62 to 2.52.

(2) Model with no environmental stochasticity (Table 3.2)

Removing environmental stochasticity from the model reduces the average population size to 99 pairs (the number of unpaired males remains the same). The variation in the data was also reduced. However, the population's growth rate was not significantly affected by removing environmental stochasticity.

(3) Model with environmental stochasticity unlinked (Table 3.2)

Simulating the effect of environmental stochasticity separately for reproduction, juvenile survival, and adult survival so that they function independently from each other results in a lower average number of pairs for the population. Number of unpaired males and the population's growth rate do not change significantly.

(4) Model with altered environmental stochasticity (Table 3.2)

The value for the mean number of pairs is less than that produced by the standard model. This is because using the standard errors for an estimate of environmental stochasticity under-estimates the variation between years.

(5) Model with altered reproductive function (Table 3.2)

The results from this model were not significant for either population size or for growth rate.

Table 3.2. Results from structural sensitivity analysis. Values show means and 95% confidence intervals. Values for population sizes and number of unpaired birds are average values taken at the 50th year after reintroduction, based on 1000 simulations. The values for growth rate are averages from the first four years based on 200 simulations. The values for the standard model are given in Table 3.1.

	(1) Model with altered program sequence	(2) Model without environmental variation	(3) Model with environmental variation unlinked	(4) Model with altered environmental variation	(5) Model with altered reproductive function
Number of pairs	103 +/- 1	99 +/- 0	100 +/- 1	99 +/- 0	102 +/- 1
Numbers of unpaired males	45 +/- 1	43 +/- 1	43 +/- 1	43 +/- 0	44 +/- 1
Number of unpaired females	0 +/- 0	0 +/- 0	0 +/- 0	0 +/- 0	0 +/- 0
Growth rate	2.52 +/- 0.20	1.62 +/- 0.04	1.61 +/- 0.04	1.61 +/- 0.05	1.60 +/- 0.05

3.4.2 Results from parameter sensitivity analysis

The effects of varying parameters were generally symmetrical (see Appendix C for graphs where the parameters are altered by up to 3 standard errors). There are some exceptions. For example, when the density dependent parameter for juvenile survival is set at -1.96 standard errors from the estimate, this results in an average population size of 75 pairs. At +1.96 standard errors from the parameter estimate, the average population size is 161 pairs (see Table 3.4).

Changing the parameters by +/- 1.96 standard errors from their estimates had a

Table 3.3. Values from sensitivity analysis of the model of the Mokoia Island Saddleback population. Values show means and 95% confidence intervals. Values for average population size are determined from 200 simulations. All values for growth rate are from 200 simulations. The standard model had an average population size are 103 pairs (+/- 1), and an average growth rate of 1.62 (f +/- 0.05).

Parameter varied	Parameter value at -1.96 s.e.	Parameter value at +1.96 s.e.	Average population size at -1.96 s.e.	Average population size at +1.96 s.e.	Average population growth at -1.96 s.e.	Average population growth at +1.96 s.e.
Density Dependent parameter (birth)	-0.032	-0.002	91 +/- 2	116 +/- 3	1.58 +/- 0.04	1.68 +/- 0.05
Intercept value for births	2.400	4.056	99 +/- 2	109 +/- 3	1.55 +/- 0.04	1.68 +/-0.06
Value for year 1 males	-0.087	-0.621				
Value for year 2 and older males	0.087	0.621	99 +/- 2	105 +/- 2	1.62 +/- 0.05	1.63 +/- 0.05
Value for year 1 females	-0.804	-1.290				
Value for year 2 and older females	0.804	1.290	98 +/- 2	105 +/- 2	1.62 +/- 0.05	1.63 +/- 0.05
Density dependent parameter (survival)	-0.046	-0.019	75 +/- 2	161 +/- 3	1.52 +/- 0.05	1.73 +/- 0.04
Intercept value for adult survival	4.254	5.132	95 +/-2	106 +/- 2	1.56 +/- 0.05	1.74 +/- 0.05
Intercept value for juvenile survival	3.604	5.279	77 +/- 2	129 +/- 3	1.49 +/- 0.04	1.72 +/- 0.05
Sex ratio	0.375	0.4453	101 +/- 2	102 +/- 2	1.59 +/- 0.05	1.65 +/- 0.05
Both Density dependent parameters varied			69 +/- 1	192 +/- 5	1.50 +/- 0.05	1.84 +/- 0.05
Adult and Juvenile survival beta values both varied			70 +/- 2	134 +/- 3	1.44 +/- 0.04	1.738 +/- 0.05

cases at $p < 0.05$. Parameters that did not have a significant effect on the average population size when varied were: male and female age class values and the sex ratio. The parameters that did not produce a significant effect on the population's growth rate when varied were: male and female age classes, the sex ratio, and the adult survival parameter.

The parameter sensitivity analysis indicated that some of the parameters do interact, and produce results greater than the sum of them altered individually (examples of this are in Table 3.3, where two circumstances were looked at).

Pair Quality (reproduction equation)

Varying the standard deviation for pair quality had minimal effect on the outcome of the model when it was multiplied by values from 0.5 to 2. Beyond this there was a gradual increase in the average number of pairs, and the growth rate. When the value of the standard deviation for pair qualities was multiplied by 5, the average population size and growth rate both significantly increased above those for the standard model although the proportional increase was slight. When the standard deviation was multiplied by 0, the growth rate increased slightly but the average number of pairs did not change significantly.

Table 3.4. Changes in population size and growth rate with changes in standard deviation of pair quality. Growth rate is the average value for the first four years, and population size is measured at the end of the 50th year after reintroduction. The estimated value of the standard deviation of pair quality is 1.26. These results are from 200 simulations.

Standard deviation for pair quality	0	0.63	1.26	1.89	2.52	3.78	6.3
Multiplication factor	0	0.5	1	1.5	2	3	5
Average number of pairs	104 +/- 2	105 +/- 2	103 +/- 2	102 +/- 2	105 +/- 2	108 +/- 3	111 +/- 3
Rate of growth	1.68 +/- 0.05	1.62 +/- 0.05	1.62 +/- 0.05	1.64 +/- 0.05	1.68 +/- 0.05	1.68 +/- 0.06	1.74 +/- 0.07

Maximum age

Altering the maximum age of the birds between 17 and 45 years had no effect on the outcome of the model.

3.5 Discussion

The purpose of this model was to identify the factors that most affected the saddleback population on Mokoia, and to assess the viability of the saddleback population. The population is viable, and is unlikely to become extinct, barring some catastrophe. The most likely catastrophe to strike the island would be the introduction of rats, which would almost certainly cause the extinction without management (Lovegrove, 1992, 1996b).

The overall population size is predicted to be just under 250 birds (103 pairs, and 44 unpaired male birds). Lynch *et al.* (1995) recommend an effective population size in excess of100, and actual sizes greater than about 1000 individuals. Populations smaller than this are thought to be at considerable risk to extinction from genetic deterioration of the population within a time span of 100 generations. An isolated population does run the risk of loosing its genetic variability over time, and while I have not included genetics in my model of the saddleback population, it should not be ignored altogether. As all populations of North Island saddleback stem from the same original island population, there should be no concerns over transferring birds between populations. The numbers of birds that would need to be transferred would not need to be very high for this to preserve the genetic variability of individual populations (Mills and Allendorf, 1996).

The mean population trends for the first five years are a close fit to the actual data from which the parameters were estimated, and they fall well within one standard deviation of the simulated data. The effects of some parameters are unclear from five and half year's worth of data. I have extrapolated from these data for values beyond this. The greatest concern is the accuracy with which the density dependence is modelled. I have fitted a simple linear decline with the number of pairs, and extrapolated. The extrapolation from the data is not great as the model predicts an average size of 103 pairs and the data covers the range from 14 to 75 pairs. It would be useful to have data from a longer period, although this may not improve the model of density dependence unless the population was again reduced to low levels. Additional data would allow better estimates of environmental stochasticity, and for environmental stochasticity to be better separated from density related effects on survival and reproduction.

As the population on Mokoia island is surrounded by water, and juveniles have free access to any point on the island, I decided against creating a spatially explicit model for the island. This would have given an alternative means to model population regulation by limiting the number of territories available by the area of the island. However, this would have required information on the relative qualities of territories for breeding. Additional data that would be required for a spatially explicit model is the dispersal behaviour of the juveniles and the searching patterns used while looking for a territory (Ruckelshaus *et al.*, 1997). These data would be needed even if only to test the hypothesis that this behaviour could be modelled simply by random dispersal from the nest. If it is not simply random dispersal, then there is the potential that it may effect the output of the model. This information would be important for any application of the model to fragmented habitat. However, it is likely to be unimportant for modelling the Mokoia Island population because there was nothing limiting dispersal within the island, and genetics was not accounted for in the model.

3.5.1 Structural sensitivity analysis

The way in which environmental stochasticity was included in the model had an impact on the average size of the population. When environmental stochasticity was left out of the model, the average population size was reduced. When the correlation between the three types of environmental stochasticity was removed, the average population size was also significantly lower than the standard model's estimate. When the three are concordant, a good year will not only see higher breeding success, but a higher recruitment rate into the population, due to higher juvenile survival. This could allow the population to reach temporarily higher levels, raising the average population size. However, this destabilisation would also decrease population viability, as the extremes of survival and reproduction will coincide, if it were under any risk.

The sequence in which the model ran affected the growth rate of the population in the first four years. When the survival function was called before the reproduction, the initial fifteen pairs were reduced before they bred. While the rate of increase in the first year was not as high, the rate in the next three years was greater, as it increased from the smaller number of pairs.

Rounding the fledglings at the level of the individual pairs, rather than the population's total, and treating negative fledglings as zero did not significantly affect the results from this model. However, it does allow the potential for some bias in the reproductive success of the population, as the normal distribution (which was assumed to fit the data), is truncated so that no values less than zero are produced. However this is unlikely to be a factor in this model as these values do not become significant until the population density has become much higher than is predicted for the population. The density dependence in the reproduction of the saddlebacks has a lesser effect on the population's size than the density dependent juvenile survival. At the population densities found in this model, the number of negative fledglings that are produced is too low to have a significant effect on the models output.

3.5.2 Parameter sensitivity analysis

Density dependence

The density dependent parameters had some influence on the growth rate within the first four years. These are the years when the population initially expands rapidly. The density dependent parameter in juvenile survival had the greatest effect of any single parameter on the population's size. Juvenile survival produced a population ceiling when the values affecting juvenile mortality were left at their best estimates. This appeared to be about 110-114 pairs (graphs in Appendix C). As the number of pairs increase; the number of juveniles surviving to become adults (over 9 months) ultimately declines to zero, and the population size reduces until the number of new recruits entering the population balances or exceeds mortality. This was not observed for reproduction at the population levels that were reached at any point in this analysis. Using the values used to calculate the number of fledglings produced per pair (Section 3.2.6), the average number of fledglings produced per pair (birds in their second year or older) reaches zero at a population density of 191 pairs.

The density dependent component in juvenile survival is likely to be due to competition for territories. Juveniles unable to obtain territories apparently have very low survival, and few floaters were observed on Mokoia Island. Once the population has increased to a size where the probability of obtaining a territory is low, then further population growth is not expected.

The estimates of the carrying capacity for the island are lower than initial estimates based on the size of the island. Lovegrove (1992) estimated that the island would be able to support up to 500 saddlebacks. From the values predicted for density dependent effects in reproduction and mortality, the expected maximum population size is about half this. O'Callaghan (1980) calculated the minimum size of a saddleback territory on Cuvier Island as being 0.45 hectares. Mokoia Island is 135 hectares in size, and this suggests that it could in theory support up to 300 pairs. However these estimates may not be entirely sensible as they are based on populations that are on other islands, where the habitat may differ, and the surveying of these populations may have been inaccurate.

Male and female age classes

The sensitivity analysis of the male and female age classes from the reproduction function examined the effect of the difference between the first year age class and the older birds. At -1.96 standard errors from the mean estimates, the difference between the two age classes was less than from the mean values. At +1.96 standard errors the gap between the two age classes was at its greatest. As the difference between the age classes increases, the possibility of negative fledglings for the first year birds increases. As this model treated all negative fledglings as zero, the average number of fledglings (from both age classes) will increase. This effect was most noticeable with the parameters for the female age classes. This effect was also seen in the variation of the distribution of pair quality.

Pair quality

When the standard deviation in pair quality was set to zero, the population's size did not change significantly. The interesting effects occur as the value of the standard deviation is increased beyond twice its normal value. Under these conditions, the average size of the population, and its growth rate begin to increase. This was probably a result of the rounding used in the reproductive function. The reproductive equation, without pair quality included, calculates the mean number of fledglings per pair. Pair quality is assumed to follow a normal distribution, so the average number of fledglings produced by a pair will be normally distributed around the mean for the population. However, because no negative fledglings are allowed in the model, this introduces a positive bias in the predicted reproductive success. As the value of the standard deviation for pair quality increases, the probability of negative fledglings being produced also increases. This will increase the mean number of fledglings produced as any negative values are truncated to zero. Under normal circumstances the effect of this is negligible (Section 3.5.1). However, as the value for the standard deviation of pair quality increase the chances of having negative fledglings also increases and this effect will become more pronounced.

Parameter interactions

When the density dependent parameters are altered together there is a marked change in the average size of the population, and the growth rate, which is more than the sum of the parts. This is not seen when both the adult survival parameter and the juvenile survival parameter are altered. Varying two parameters from within the same part of the model (such as survival or reproduction) will not influence the population more than the sums of the two individual parameter changes. However, if juvenile survival is increased, then changing parameters that effect the number of fledglings produced will have a greater effect. The population is very susceptible to changes in recruitment so that any change that affects this will have important consequences for the population.

3.6 Summary

The model produced results that closely match the observed population growth of the Mokoia Island population. This model predicts an average population size for the island of 103 pairs and 44 unpaired males, once population expansion (from the initial release) has ended. The average size of the population was most sensitive to error in the terms used to calculate juvenile survival. The population's growth rate was most sensitive to error in the terms for adult and juvenile survival. The manner in which environmental stochasticity was included into the population affected the population's average size, but did not effect the population's growth rate. These parameters are those which need to be carefully estimated, as they are the ones which show the greatest influence on the models output within their 95% confidence intervals. However, to gain more accurate estimates of these values would require several years worth of more data, particularly for environmental variation.

4

Population Management

4.0 Abstract

In this chapter I include the poison drop that occurred on Mokoia Island into the simulation model. I then extrapolate the model to a hypothetical mainland situation where poison drops are used to control predators. My aim was to assess the viability of reintroducing saddlebacks onto the mainland. The final part of the chapter explores the possibility of harvesting island populations like Mokoia for mainland reintroductions.

Including the poison drop in the model indicated that it caused no long-term effects on the population. A single poison drop did not affect the population's viability regardless of which year it occurred.

My mainland model was based on the assumption that poison drops would totally remove predators for six months and then predators would immediately return to pre-poison levels. I also assumed that a poison drop would cause the same mortality as observed on Mokoia Island. Reintroduction of saddlebacks onto the mainland is not predicted to be feasible due to mortality from the poison. Aerial drops are therefore unlikely to allow viable populations unless they reduce predators to low levels for more than six months.

I estimated the maximum number of birds that could be removed from the Mokoia Island population with it remaining viable. The Mokoia Island saddleback population can be harvested with little cost to the population. A maximum of 139 birds was estimated, for one harvest, with the population taking about six years to recover to its previous level.

4.1.0 Introduction.

In this chapter I look at two management options for a saddleback population. First I examine the potential use of poison drops for allowing saddlebacks to be released on the mainland. Secondly I assess the number of birds that could be removed from the Mokoia Island population, under several different harvesting regimes, without causing the population's extinction.

This chapter is broken down into three main sections. The first section (A) models the effect of the poison drop in September 1996 on the Mokoia Island population. The second section (B) explores the viability of a mainland release for saddlebacks. I initially examine the effects of varying the rates of juvenile survival, adult survival, and reproduction so that the minimum rates for a self-sustaining population can be found. Because it is unlikely that rats will ever be eliminated from the mainland, it is necessary to estimate the minimum values that will allow the establishment of a self-sustaining population. I then included a poison drop in the model with the reduced parameters. I looked at two poisoning regimes, annual and biennial to see how these altered the predation levels that a population could sustain. The final section (C) explores possible harvesting regimes for the Mokoia Island population, as a potential source population for future releases.

4.1.1 Rodents

Polynesian settlers brought kiore (Polynesian rat, *Rattus exulans*) to New Zealand, which appear to have eliminated several species of birds, flightless insects and some reptiles (Atkinson and Moller, 1990). From 1769 Europeans established over 80 species of vertebrates, including three additional rodent species, three species of mustelids, six marsupials, and several species of deer (Clout and Saunders, 1995). All of the rodent species are omnivorous, consuming a wide variety of animal and vegetable material (Buckle and Fenn, 1992). Norway rats (*Rattus norvegicus*) are large and fossorial, making ground dwelling birds particularly vulnerable, but they are not arboreal. It was thought that saddlebacks might be able to coexist with *R. norvegicus*, but research on reintroduced saddlebacks on Kapiti Island in the presence of *R. norvegicus* suggested that the population was not viable (Lovegrove, 1992). Ship rats (*R. rattus*) are adept climbers and prey on birds, both on the ground and in trees. They are the most devastating to birds, and saddlebacks do not co-exist with them. *R. exulans* is the smallest of the three rat species. It can take birds from on the ground or aboreally, but it usually takes smaller prey. Saddlebacks have had variable success with *R. exulans*, thriving with them in some locations, but possibly being eradicated by them on others (Lovegrove, 1996b). *Mus musculus* is the smallest rodent in New Zealand. The house mouse is omnivorous, and is preyed on by the other three rodent species. Saddlebacks do not appear to be threatened by mice.

There are several techniques used to control rodents in the wild: trapping, ground based poisoning, and aerial poisoning. Trapping is more labour intensive than poisoning, and less successful in most situations (Moors *et al.*, 1992). However, it does play a part in eradication programmes. Ground-based poisoning is more costly per hectare than aerial poisoning, but it can be used to target specific areas such as nest sites

(Innes *et al.*, 1995). Eradication using these techniques is only possible on offshore islands, outside the natural swimming range of exotic predators (Veitch and Bell, 1990). On the mainland, these techniques only reduce predator populations, as reinvasion from areas outside the management zone will occur. Aerial and ground based poisoning operations can reduce ship rat abundance by up to 90% (Innes *et al.*, 1995). In the long term, the best prospects for broad scale restoration on the mainland lie with biological control rather than the perpetual use of traps and poisons (Clout and Saunders, 1995).

The largest threat to the Mokoia Island population is the establishment of either the Norway or the ship rat on the island. These predators can take young and eggs from the nest, and they can also kill adults at the nest or from roost sites.

4.1.2 Use of brodifacoum in rodent control

Brodifacoum is a widely used poison for the control of rodents in New Zealand. It has also been used to control rabbits (*Oryctolagus cunniculus*), wallabies (*Macropus* sp.) and brushtail possums (*Trichosurus vulpecula*) (Eason and Spurr, 1995; Eason *et al*, 1993). Brodifacoum, is an anti-coagulant that acts by interfering with the normal synthesis of vitamin K dependent clotting factors in the liver of vertebrates (Hadler and Shadboldt, 1975).

Brodifacoum is extremely insoluble in water (<10 mg/litre of water at pH 7). When the baits disintegrate, brodifacoum is likely to remain in the soil, where it may slowly be degraded by soil organisms (Ogilivie *et al.*, 1997). The half-life of brodifacoum in soil under aerobic conditions is estimated to be 157 days (WHO, 1995).

Because brodifacoum is a slow acting poison, taking several days to kill once a lethal dose has been ingested, there is a risk of secondary poisoning to other organisms if they eat the species ingesting the bait. Alterio (1996) recorded secondary poisoning of stoats, ferrets, and cats after a brodifacoum-poisoning programme aimed at rabbits. Secondary poisoning can therefore be effective at removing predators (Alterio *et al.*, 1997). However, there is also a risk to native predators such as the morepork (*Ninox novaseelandiae*) (Stephenson *et al.*, in press).

Invertebrates have been recorded eating baits containing brodifacoum, and residues of brodifacoum have been found in beetles (Coleoptera) collected from bait stations on Stewart Island (unpublished data cited in Eason and Spurr, 1995). Brodifacoum residue has been detected in tissue from insects found on baits (Ogilivie *et al.*, 1997). The secondary poisoning of insectivorous birds with brodifacoum has been recorded, where birds of several species died in an aviary after eating ants and cockroaches that had consumed brodifacoum baits (Godfrey, 1985). This presents a potential problem for saddlebacks, as they are insectivorous and could suffer secondary poisoning from consuming poisoned insects.

In a test of which native birds would be likely to consume poison baits, Spurr (1993) found that the saddleback would consume baits used for aerial poison drops. This was attributed in part as natural curiosity towards a novel food item. They also trialed cinnamon flavoured baits to see if this discouraged native birds from ingesting them, but this did not work with saddlebacks, which readily ate both baits. However, this trial was conducted using captive birds, which may alter the bird's behaviour, and there were only five saddlebacks used in the trial.

4.2 A. Incorporating the poison drop into the model

The simulation model described in Chapter 3 was modified to include the poison drop. The poison drop occurred on 18 September 1996, which was one month before the first eggs were recorded in the nest boxes (20 October 1996). The decreased survival was measured in the month following the poison drop. At the time of the poison drop there was a maximum of 30 marked birds alive that were classified as juveniles (first nine months after becoming independent from their parent). These birds were the last fledglings from the 1995-96 breeding season, which consisted of 52 marked birds.

The standard model (from Chapter 3) calculates the survival probability for one month. This value is then converted into an annual probability by raising it to the power of 12 (see Section 3.2.5). To incorporate the poison drop into the model, the survival function was altered for the designated year of the poison drop. For each age class, this function calculated the normal survival probabilities for 11 months. For the juvenile birds, this consisted of nine months of normal juvenile survival and two months of normal adult survival. For the adult birds, this was their normal survival probability (which remained constant except for environmental variation) for 11 months. The survival for the month after poisoning was then calculated. These two values (normal 11 month survival and survival for the month after the poison drop) for each age class were then multiplied to produce an annual survival estimate.

If the month in which the fledglings enter the population is considered to be January then the month in which the poison takes place is October. This is different from the actual events where the poison was dropped in September. Allowing a poison drop to occur one month before the first eggs are laid, and then allowing two months for the young to develop and to reach independence, places the poison drop three months before the juveniles are considered to be independent (January). The results from the poison drop (decreased survival) will be felt in the tenth month, which is October. This also resulted in juvenile survival for that month being calculated using the adult term for the poison effect. This was because birds were considered to be juveniles for nine months, before becoming adults for the calculation of survival probabilities. Using October as the time for the simulated poison drop results in only the adult values for decreased survivorship being used. This is largely a consequence of the structure of the model. All birds are treated as becoming independent fledglings (the value used to simulate reproductive success) on the same date in the model, whereas in reality the dates on which saddlebacks fledge can be spread over approximately one half of the year (see Section 1.2).

Using the estimate of the poison's effect on juvenile survival was complicated, as juvenile survival is not linearly related to the number of breeding pairs (Figure 3.1). Using the logit link function to express survival as a probability means that the effect of the poison does not remain constant as the number of pairs in the population varies (Figure 4.1). The number of pairs at the time of the poison drop was estimated to be 75 pairs. This is potentially a problem, as further on in this chapter the poison effect will be applied to different population densities. Using the poison term estimated for adult birds, and described above avoids this. This can be justified as both terms produce similar survival estimates (Table 4.1).

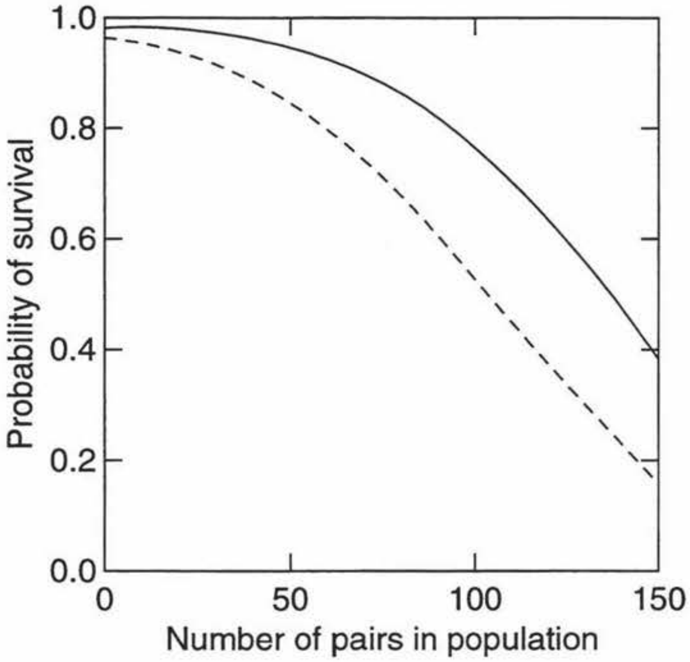
The estimate of the poison's effect on the adult age class is more robust, as adult survival is density independent, and there was a much larger sample size. The estimate of poison effect on adult birds is applicable to the population at any density. It also makes more sense logically to use the tenth month to incorporate the effects of the poison as this simulates a poison drop just before the breeding season begins.

Table 4.1. Parameter estimates for poison effects plus estimated survival probabilities for the Mokoia Island population. Survival estimates are for one month, and the number of pairs for the juvenile survival estimate is 75.

Parameter	Beta value	Standard error	Monthly survival estimates	
			With Poison	Without poison
Adult poison effect	-3.687	0.311	0.730	0.990
Juvenile poison effect	-1.099	0.898	0.710	0.880

I performed a sensitivity analysis to see how varying the poison parameter affected the population. This was achieved by varying the β value for the poison effect in the survival equation by +/- 1.96 standard errors. This was only done for the adult poison effect as I only use this value in my simulation model as described above. The effect of varying the poison effect was measured in terms of the numbers of pairs that were alive

Figure 4.1. Comparison of monthly juvenile survival with poison (dashed line) and without the poison (solid line).



after the survival function was called, in the year of the poison drop. I also varied the year in which the poison drop occurred, to see if poisoning might be a greater threat to the population's viability while the population was small immediately after reintroduction. The initial population size for all parts of this sensitivity analysis was 20 unpaired males and 16 unpaired females (the size of the initial founder group on Mokoia Island). 1000 simulations were run, where the population was simulated for six years after the reintroduction.

4.2.1 Results

Incorporating the poison drop into the model produced results that were close to the population growth observed on Mokoia Island (Figure 4.2). There are only discrepancies for the number of pairs at the start of the 1995-96 season (before the poison drop), and for the number of pairs in the 1996-97 season (just after the poison drop). However, both of these results are within one standard deviation of the average number of pairs predicted for each year.

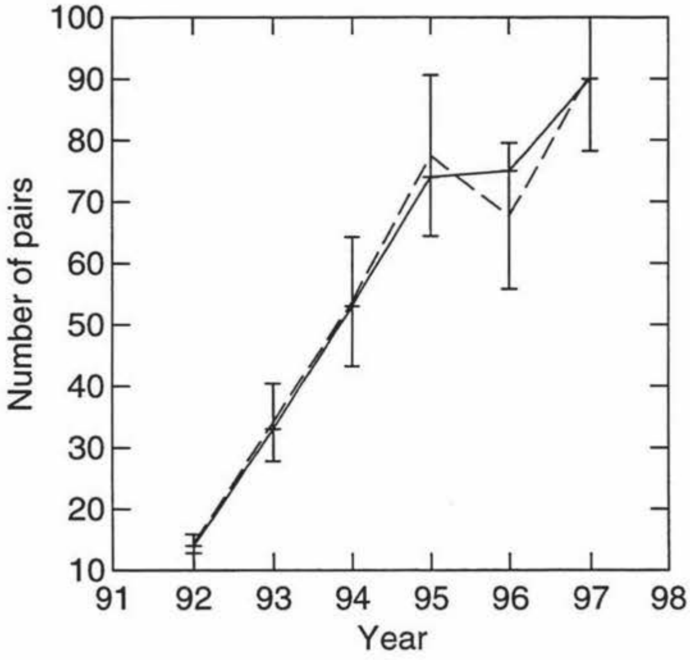
The probable cause of these deviations is that the model structure differs from reality. The population processes occur continuously, whereas my model uses discrete time steps of one year to model the population. All functions are applied instantaneously to all individuals, in the order specified by the model's structure.

The sensitivity analysis produced an average number of 54 pairs (0.4 s.e.) at -1.96 standard errors and 78 pairs (0.4 s.e.) at +1.96 standard errors for the year of the poison drop. Not including the poison drop in the model produces 91 pairs (0.4 s.e.), in the fifth year from release (Figure 3.4).When the poison drop is included in the model, 91 pairs is reached in the sixth year (Figure 4.2). Altering the timing of the poison drop from year one to year six did not cause population extinction at any time.

4.2.2 Discussion

The results show that about 73% of the adults survived the month after the poison drop. This is much worse than the standard monthly survival rate of 99%. The post-poison survival rate was similar for birds classified as juveniles (Table 4.1). Normal monthly juvenile survival is 88% (for the population density recorded at the time of the poison drop) compared to the higher adult survival (99%). This suggests that juveniles were not affected by the poison drop to the same degree as adult birds were. However, this is probably due to the fact that these birds were nearing the end of the time when they were classified as juveniles and their normal survival rate would have been similar to that observed in adults. In addition, the juvenile sample size for this event is low, with a maximum of 30 banded birds available to estimate this value, and not all of these would have survived to the poison drop.

Figure 4.2. Population trajectory predicted from the simulation model compared to the counts of pairs on Mokoia Island. The solid line is the number of pairs during each breeding season. The dashed line is the mean number of pairs during each breeding season from the simulation, with error bars showing one standard deviation either side of the mean. "Year" is the year at the start of the breeding season.



The simulation results show that the poison drop delayed population growth by one year, as the population averages 91 pairs in the sixth year (Figure 4.2) as opposed to the fifth year when the poison drop is omitted (Figure 3.4). The poison did not endanger the population, and there were no extinctions in any of the simulations run. Increasing the additional mortality of the poison drop by decreasing the β term by 1.96 standard errors also did not cause the population to go extinct.

In summary, while the population will suffer decreased survival immediately after a poison drop, it will not suffer any long-term consequences from a single drop.

4.3 B. Is reintroduction onto the mainland feasible?

Reintroducing the saddleback onto the mainland is unlikely to succeed without human intervention to aid the species. The most obvious management techniques that could be used are aerial poison drops to control predator populations. Additional aid in the form of predator-proof nest and roost boxes might also help the species to some degree (Lovegrove, 1992), as might ground-based poison bait stations around nest sites.

In this section I look at the effects of altering population parameters to simulate the effects of predation from introduced predators. The data from Mokoia Island probably include the effect of some predation from native species in the estimates of survival. Mokoia Island has morepork and weka (*Gallirallus australus greyi*), both of which prey on saddlebacks (weka can catch saddleback young on the ground). On the mainland, saddlebacks would also be at risk from introduced predators such as rodents, mustelids, cats, dogs, and possums. There have also been reported cases of nest robbing by starlings (*Sturnus vulgaris*), where saddleback eggs are destroyed (Lovegrove, 1992).

Innes *et al.* (1999) used an adaptive management approach for the kokako on the mainland. They were able to increase the reproductive success and viability of these populations through the use of predator control programmes. Predators have been linked to declines in native species (Wilson *et al.*, 1998; Buckle and Fenn, 1992; Moors, 1985), so these must be reduced to enable endangered native species such as the saddleback on to the mainland. Eradication techniques are only effective on islands outside the natural swimming range of the predators (Veitch and Bell, 1990), but similar techniques can be used to control predator populations and to reduce their densities on the mainland.

As the poison drops will also kill saddlebacks and other non-target species, it is not a simple matter to just use poison to control predators.

There are two questions to be considered when planning a poisoning programme:

(1) What minimum rates for survival and reproductive success are required for a self-sustaining population?

(2) At what point do the potential benefits of the poison drop become offset by the increased mortality related to the poison drop?

To look at the usefulness of the poison drops I needed to vary survival and reproductive success to simulate the effects of predators. The poison becomes useful when it allows saddlebacks to survive in circumstances where a population would otherwise have gone extinct.

4.3.1 Simulating a population under predation pressure

I began this analysis by varying the three parameters of interest (juvenile survival, adult survival, and reproductive success) individually. The reason for this was see how the population responded to changes in each of these parameters. The second stage was a more in-depth look at varying the parameters so that the effects on the probability of extinction for a founder group of 20 pairs. The third stage was to add the poison drop and to see how this altered the results from the previous stage.

4.3.1.1 Varying juvenile survival, adult survival, and reproductive success (stage 1)

To conduct the first part of the analysis, I modified the main program so each parameter could be varied. The values that I used to alter the parameters ranged between zero and one. This value was multiplied against the normal estimate of that parameter (juvenile survival, adult survival, or reproductive success), to produce a proportion of the normal value for that parameter, which was then used in the model. The reason for altering the parameters by a proportion was that both juvenile survival and reproductive success vary with the number of breeding pairs in the population.

I recorded the average population size that was reached for various proportions of the parameters. Where there was a chance of extinction for a particular parameter value the population was considered to have an average population size of zero.

The models used for this analysis ran 200 simulations from which the average population size was determined. As this is a stochastic model, the average number of pairs varies from year to year (Figure 3.2). The average population size was the mean size around which the population would fluctuate, once it had finished its initial growth phase. The average population size was calculated from 200 simulations. For all occasions where I calculated the population's average size, I ignored the population's initial growth phase and only used the value where the mean remained relatively constant for 20 years, with no upward or downward trends. The starting population was 20 pairs.

4.3.1.2 Assessing reintroduction viability (stage 2)

To assess the viability of reintroduction I initially ran a series of scenarios, where parameters were reduced, to assess the minimum parameter combinations that would support a viable population. I varied reproductive success versus survival, and recorded the average population size reached for each parameter combination. Adult and juvenile survival were always reduced by the same proportion, e.g. if the proportion was set to 0.5 then adult survival was half of what it was normally and juvenile survival was half of its normal value for each particular population density. Each parameter was reduced, and for each of these scenarios 200 simulations were run, and the average population size (determined from the 200 simulations) was recorded when it remained approximately constant for 20 years (as described in Section 4.3.1.1). If one or more populations became extinct then the population size was recorded as zero.

Once the minimum values for a self-sustaining population had been graphed, I looked at extinction probabilities for a reintroduced population. This part of the analysis required varying the three parameters to estimate the effects on the viability of a reintroduction. While it was possible to alter all three parameters together within the body of one program, it would have been difficult to present this in an easily understandable fashion. Instead, I produced a collection of two-dimensional graphs with contour lines marking the parameter combinations that result in specified extinction probabilities. These values indicated where the population had a 90%, 50%, 20% and 0% chance of extinction over 20 years from reintroduction.

The parameter combinations used were:

(1) Reproduction versus survival, with both adult and juvenile survival reduced by the same proportion (Figure 4.7).

(2) Juvenile survival versus adult survival, with reproductive success reduced by 25% (Figure 4.8A).

(3) Juvenile survival versus adult survival, with reproductive success reduced by 50% (Figure 4.8B).

(4) Juvenile survival versus adult survival, with reproductive success reduced by 75% (Figure 4.8C).

The sensitivity analysis of the simulation model in Chapter 3 had identified three variables that had the greatest impact on the model's outcome (Section 3.4.2). Since uncertainties in these variables could affect my estimate of the viability of mainland reintroductions, I needed to assess their impact on the extinction contours for the predator-affected populations. The three variables were: the density dependent term in the juvenile survival equation, the juvenile survival intercept term, and the adult survival intercept term. Each of the three term's identified was altered to the extremes of the 95% confidence interval for the estimate of the terms value, and then the model for combination (1) above was then run with these altered values. However, the affect of the three terms was only assessed at the 0% and 90% extinction contours (Figure 4.9A-C).

The starting population size for this analysis was 40 birds (20 male, 20 female) just released into the new reserve. This is a typical number for a reintroduction of forest birds in New Zealand (Armstrong and McLean, 1995). Each time the model ran 200 simulations for each parameter combination.

4.3.1.3 Incorporating the poison drop into the reintroduction models (stage 3)

I assumed that the poison would have an all or nothing effect on the predator populations. During the six-month period following the poison drop, survival and reproduction were at normal values. The poison was dropped three months before the independent fledglings were added to the model, to simulate a poison drop before the breeding season begins, allowing three months for eggs to be laid and nestlings raised, with three months of normal survival for juveniles. After this six-month period the survival rates were again reduced by the specified proportions. The poison was incorporated into the models to assess the effect on the extinction contours.

The parameter combinations that I ran were:

(1) Reproduction versus survival, where adult and juvenile survival were both reduced by the same proportion, with annual poison drops. As the poison drops were annual, the model assumes that the poison drops allow a normal reproduction rate (Figure 4.10A).

(2) Reproduction versus survival, where adult and juvenile survival were both reduced by the same proportion, with biennial poison drops (Figure 4.10B).

(3) Juvenile survival versus adult survival, with annual poison drops (Figure 4.11).

(4) Juvenile survival versus adult survival, with biennial poison drops and reproductive success reduced by 25% in the non-poison year (Figure 4.12A).

(5) Juvenile survival versus adult survival, with biennial poison drops and reproductive success reduced by 50% in the non-poison year (Figure 4.12B).

(6) Juvenile survival versus adult survival, with biennial poison drops and

reproductive success reduced by 75% in the non-poison year (Figure 4.12C).

4.3.2 Additional model assumptions for the inclusion of the poisoning data

Incorporating the poison drop into the model and using it to analyse the viability of populations on the mainland required several assumptions to be made in addition to those already discussed in Section 3.2.9.

(1) *The effectiveness of the poison*

As noted above, I assumed that the poison drop was 100% effective, allowing normal survival and reproduction for six months (six months with survival reproduced, five months of normal survival, and one month with the poison drop. It is more likely that the saddleback population would be subjected to a graded effect, where the predator populations slowly increase back up to their previous levels after the poison drop.

A long-term poisoning program also runs the possible risk of the target species developing some immunity to the poison. This can occur where animals that are not affected by the poisoning program on the periphery of the target zone.

(2) *Mainland reserve of the same size as Mokoia*

I assumed that the size of this hypothetical mainland reserve is of the same size as Mokoia Island (135 ha), so that the population will experience the same growth curves as it did on Mokoia Island. At a larger site, the population will take longer to reach a higher density. This assumption also implies that habitat use and the factors affecting population density will be similar in the new location.

(3) *A continuous poisoning regime over two decades.*

I assumed that the poisoning program occurred over a period of two decades.

(4) *No long-term effects of poisoning on the saddleback population*

I assumed that sub-lethal doses of the poison would not affect the saddleback's reproductive success. Brodifacoum has been found to cause abortions in sheep at sub lethal doses (unpublished data cited in Godfrey, 1985), so the assumption of no effect is not necessarily valid. However, the reproductive success on Mokoia Island during the breeding season after the poison drop (1996-97) was similar to the previous season where the density was similar (compare values for 1995-96 and 1996-97, Figure 2.2). Therefore there is no evidence of sub-lethal poison doses of brodifacoum affecting the saddleback's reproductive success on Mokoia Island.

I also assumed that there were no cumulative effects on survival. Substantial brodifacoum residues can remain in animal tissue for several months after poison has been dropped (Murphy *et al.*, 1998; Eason *et al.*, 1996). This means that a sub-lethal dose may accumulate and become fatal over a long period of time. Therefore it's possible that poisoning might have a higher impact on cohorts previously exposed to it.

4.3.3 Results

4.3.3.1 Varying juvenile survival, adult survival and reproductive success (stage1)

Population viability was predicted to be more affected by adult survival rates than by juvenile survival or reproductive success. Adult survival needed to be at least 40% of its normal value to allow a 100% chance of a sustainable population (Figure 4.3). Varying the juvenile survival rate and reproductive success by the same proportions produced almost identical curves (Figure 4.4 and Figure 4.5). For both juvenile survival and reproductive success, the parameter could be reduced as low as 9 percent of its normal value with there still being a sustainable population. In both cases, the average population size was about 25 pairs, whereas the average population size at the minimum value for adult survival was 32 pairs. These results are influenced by the longevity of the saddleback. If the adult survival rates remain high, a population can be sustained with substantially reduced juvenile survival or reproduction.

4.3.3.2 Assessing reintroduction viability (stage 2)

Looking at the average size of a viable population shows a steep decline from the highest value, when both survival and reproductive success are at normal values to a minimum value of 25 pairs (Figure 4.6). As this figure is for average population size, the lowest contour on the graph represents the minimum values for the parameters to allow a viable population.

As reproduction decreases the survival rates needed for a viable population increase (Figure 4.8A-C) the area contained within the 0% extinction contour decreases. When survival is treated as one value with both juvenile and adult survival varied by the same proportion, it is slightly skewed. The population remains viable with a reduced rate of reproduction, in comparison to the same degree of reduction in survival (Figure 4.7). Separating adult and juvenile survival, with reproductive success reduced to set levels (25%, 50% and 75%) shows a similar skew, with adult survival limiting the population's viability to a greater extent than juvenile survival does (Figure 4.8).

Altering the value for the density dependent term in the juvenile survival equation had no effect on the extinction contours (Figure 4.9A). The juvenile survival intercept and

Figure 4.3. Average population size plotted against the proportion of standard adult survival. The population went extinct where the proportion was less than 0.4 (i.e. best estimates of adult survival).

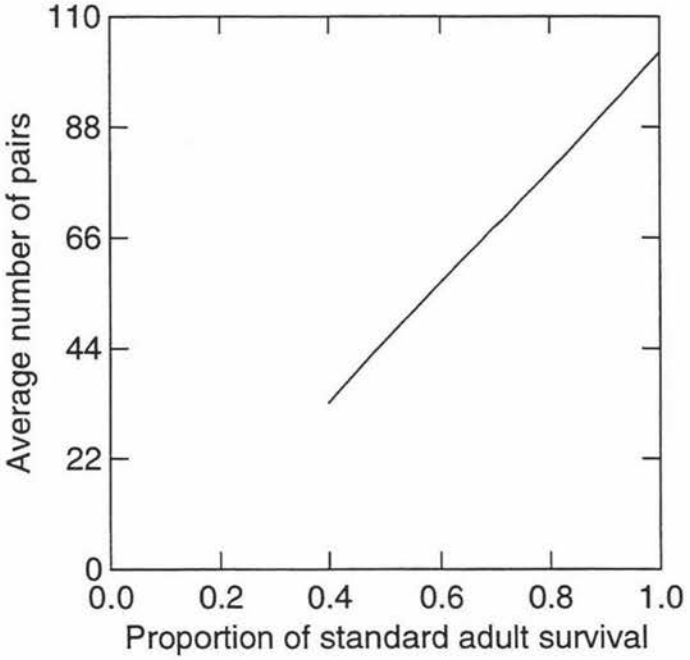


Figure 4.4. Average population size plotted against proportion of standard juvenile survival. The population always went extinct when the proportion was less than 0.09.

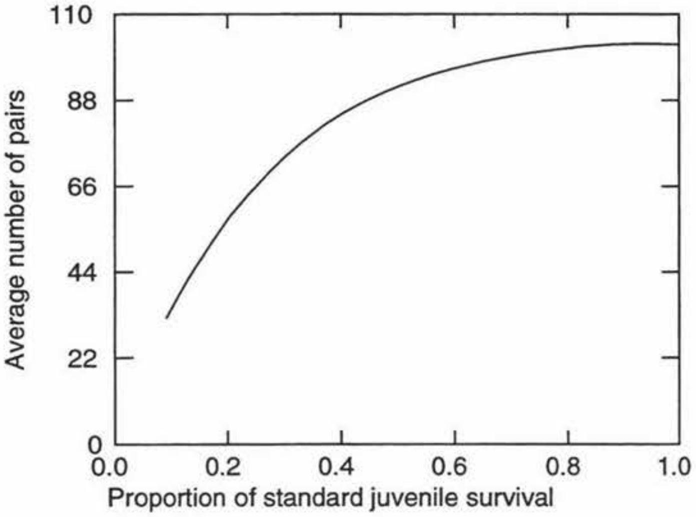


Figure 4.5. Average population size plotted against proportion of standard reproductive success. The population always went extinct when the proportion was less than 0.09.

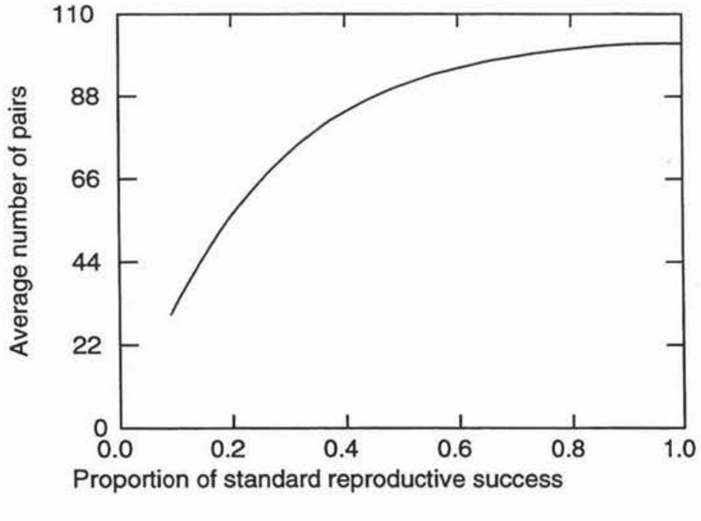


Figure 4.6. Average population size plotted against proportions of standard reproductive success and survival (where the same proportion is applied to both adult and juvenile survival). The population went extinct where the population size was less than 25 pairs. The contours on the graph represent the increasing number of pairs, with each contour equal to 2.5 pairs.

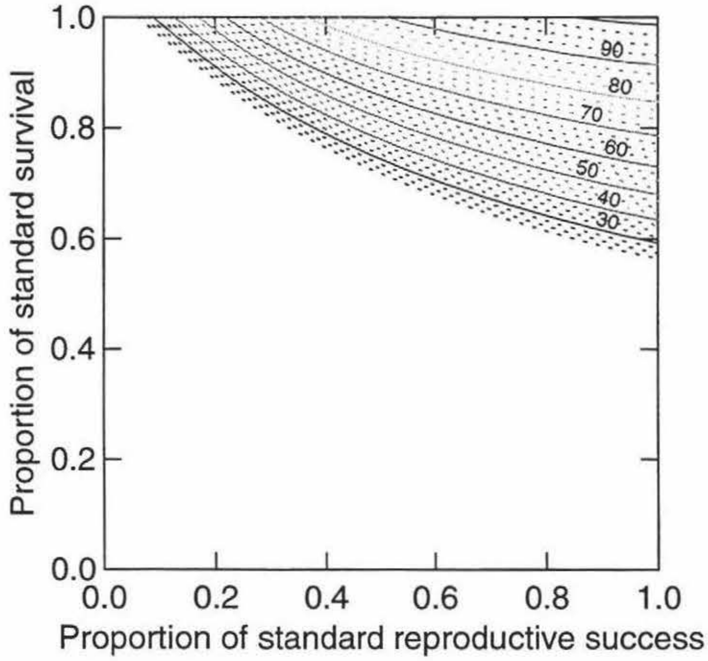


Figure 4.7. Probability of extinction as reproductive success and survival (adult and juvenile) are reduced. Contours are 0%, 20%, 50%, and 90% probability of extinction.

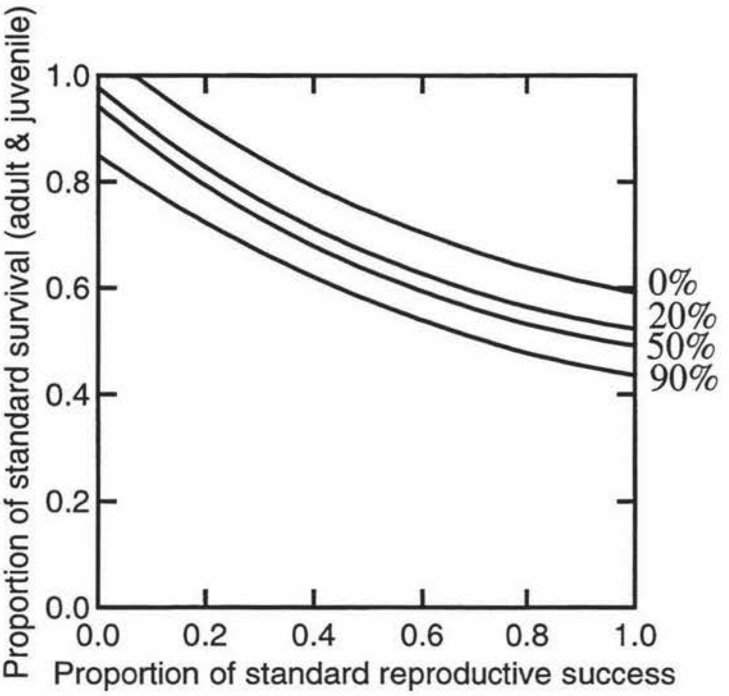
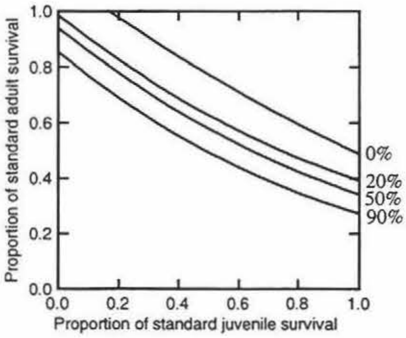
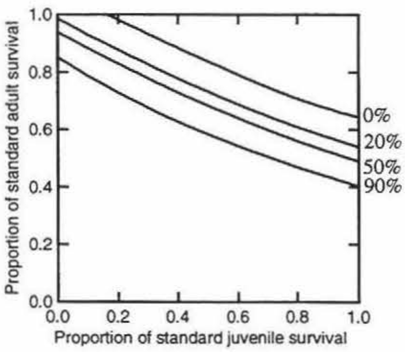


Figure 4.8. Probability of extinction as juvenile survival and adult survival are reduced. The proportion of normal reproductive success has been varied for each version of this graph. Contours shown for 0%, 20%, 50%, and 90% probability of extinction.

A. Reproductive success reduced by 25%.



B. Reproductive success reduced by 50%



C. Reproductive success reduced by 75%.

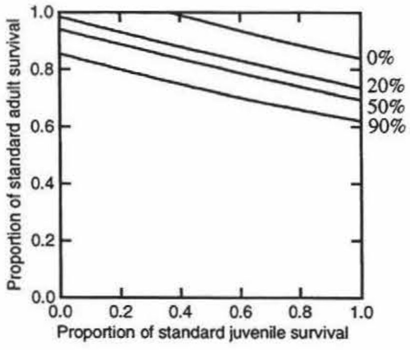
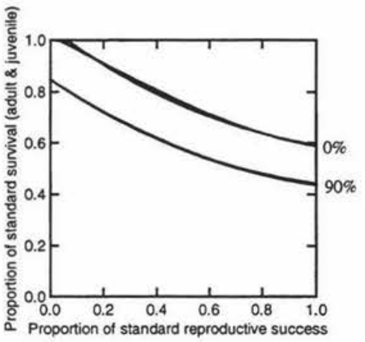
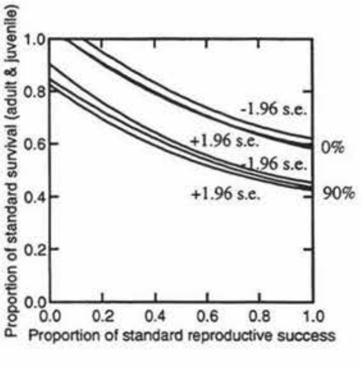


Figure 4.9. Sensitivity analysis for predicted effects of survival and reproduction on probabilities of extinction. On each panel, three contour lines are shown for 0% and 90% probabilities of extinction. The middle contour shows the values determined with the best estimates of the parameters. The upper and lower contours show the change in predicted values as a parameter is increased by 1.96 standard errors, or decreased by 1.96 standard errors. The parameters were (A) the juvenile density dependent survival term, (B) the adult survival intercept term, (C) the juvenile survival intercept term.

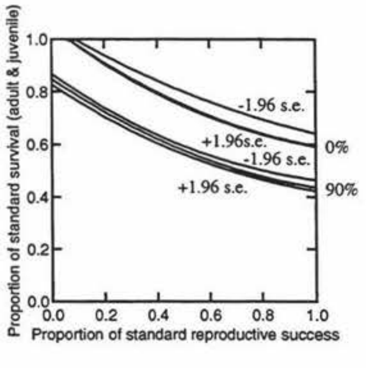
(A) Juvenile density dependent survival term



(B) Adult survival intercept term



(C) Juvenile survival intercept term



the adult survival intercept altered the positions slightly for the 0% and 90% extinction contours.

One apparent anomaly from these graphs is that with zero reproduction, or juvenile survival, there still appears to be some chance of the population surviving (less than 100% extinction). This is because the extinction probabilities are only measured for 20 years. Because the saddleback can be long-lived, it is possible for some of the founders to survive for the entire 20 years. The most useful contour to look at is the 0% extinction contour, as this indicates those parameter estimates that did not result in any extinctions within 20 years from 200 simulations.

4.3.3.3 **Incorporating the poison drop into the reintroduction models** (stage 4)

Comparing Figures 4.9A & B (annual poison drops, biennial poison drops, reproduction and survival) and 4.7 (reproduction and survival) shows the effect of the poison drop on the extinction contours. Including the poison drop has widened the gaps between the extinction contours. Annual poisoning allows normal reproduction, so these contours are straight lines (Figure 4.9A). The zero percent extinction contour has moved up, meaning that with the poison drop the population will need to have lower survival or higher reproductive rates to have a 0% chance of extinction. However, the other contours have moved downwards, increasing the area within each of the extinction contours for the 90%, 50% and 20% chance of extinction within 20 years. If there is a significant impact of predation on reproduction, then annual poisoning is a better approach than biennial.

Comparing Figure 4.11 (adult survival and juvenile survival with annual poison drops) and Figures 4.8A-C (adult and juvenile survival at reproductive success rates of 0.75, 0.5, and 0.25) shows that the poison drop widens the gaps between the extinction contours. When reproductive success is not affected to a large degree (i.e. reduced by about 25%), then biennial poisoning is a better approach than annual poisoning (Figure 4.12).

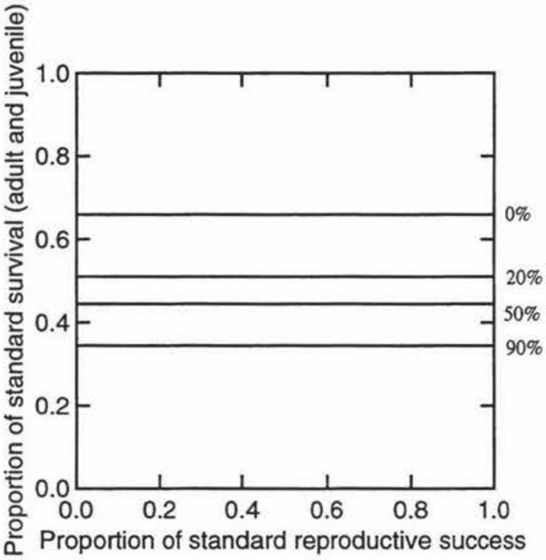
4.3.4 Discussion.

The poisoning did increase the population's viability to a degree. However, the increased reproductive success enabled by annual poisoning drops, and the increased survival for six months after the poison drop did not offset the mortality induced by the poison very much (Figure 4.10A compared to Figure 4.7, Figure 4.11 compared to Figure 4.8).

Using poison to reduce potential predation pressure on the saddlebacks will under some conditions increase the viability of a population. When the effect of predation on

Figure 4.10. Probability of extinction as reproductive success and survival (adult and juvenile) are reduced, when there is an (A) annual, or (B) biennial poison drop. Contours shown are for 0%, 20%, 50%, and 90% probabilities of extinction.

A. Annual poison drops.



B. Biannual poison drops

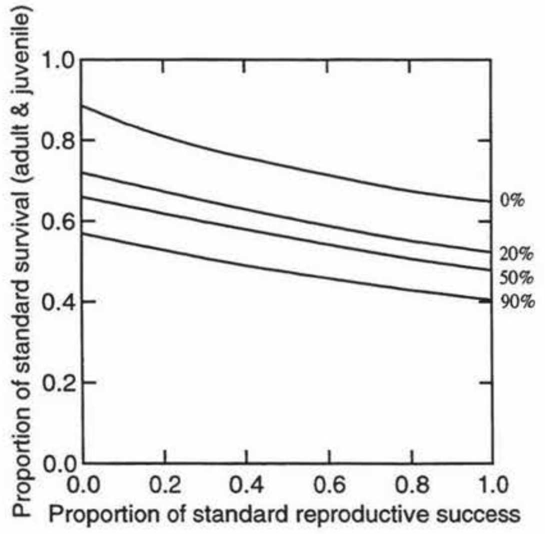


Figure 4.11. Probability of extinction as adult survival and juvenile survival are reduced, when there is an annual poison drop. Contours shown are for 0%, 20%, 50%, and 90% probabilities of extinction.

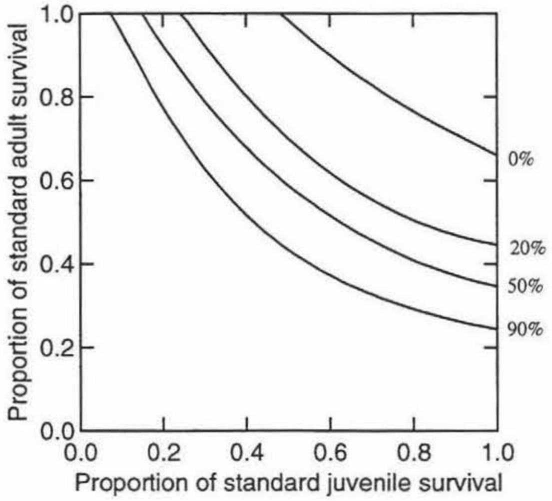
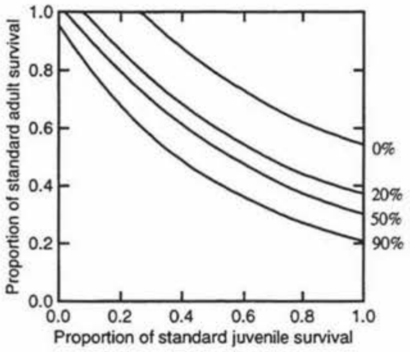
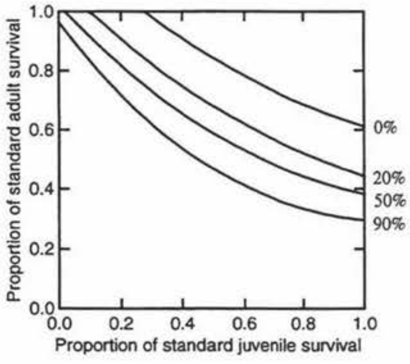


Figure 4.12. Probability of extinction as juvenile survival and adult survival are reduced, when there is a biennial poison drop. The proportion of normal reproductive success has been varied for each panel. Contours shown are for 0%, 20%, 50%, and 90% probability of extinction

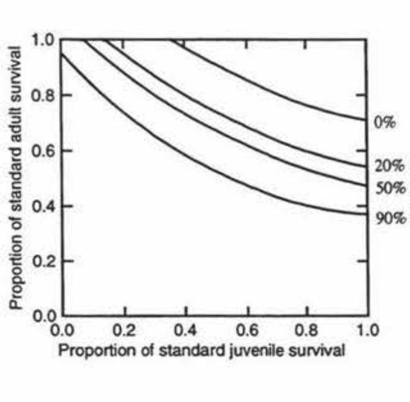
(A). Reproduction reduced by 25%



(B) Reproduction reduced by 50%



(C) Reproduction reduced by 75%



reproduction was greater than the effect on adult and juvenile survival (Figures 4.8C and 4.10a), then annual poison drops were most useful. When reproductive success is not greatly reduced, but adult survival and juvenile survival are affected, then the best approach is biennial poisoning (Figure 4.12). However on the mainland, it is likely that all three parameters, juvenile survival, adult survival and reproductive success, will all be greatly reduced.

I suspect that the actual predation levels likely to be encountered on the mainland will be outside the contours predicted for 0% extinction probabilities. My general conclusion from this analysis is that the saddleback will not be able to be reintroduced onto the mainland, unless predators can be substantially reduced for long time periods.

This model was based on the assumption of being able to reduce predator populations to zero for six months following a poison drop. If a control programme were able to have a longer-term effect, then the possibility remains open for reintroduction to the mainland. Innes *et al.* (1995) that rats took between 2-5 months to re-invade an area of 3200 ha. Alterio (1996) found stoat trails nine weeks after a brodifacoum-poisoning programme. Assuming that it takes six months for the area is likely to be optimistic unless reinvasion is particularly slow, such as might be found on a peninsular, or the area is very large.

The results from the first stage of this analysis show that adult survival is important for the survival of a population, more so than juvenile survival. As the saddleback is a long lived species, a pair might only need to produce two fledglings in ten years to replace themselves. While this is simplistic, it highlights the point that if adult survival is high then juvenile survival can be low with the population remaining viable. This compares with results from previous studies on kiwi and kokako, both of which have long-lived adults (but differ from the saddleback in that their adults are larger and better able to defend themselves against predators). McLennan *et al.* (1996) found that the extremely low survival (through predation) of kiwi juveniles was the major cause of the species' decline. Innes *et al.*, (1999) found that predator control operations helped the reproductive success of the kokako, enabling populations to increase in size on the mainland. In these situations is a high predation rate on the juveniles, resulting in a low recruitment rate. As a result there are not enough young birds joining the population, so it slowly declines as the older birds die.

The important question is whether the cost of a continued large scale-poisoning program is feasible with the costs involved. Solely for a saddleback population, I would guess that such management might not be cost effective, but if the area being managed also contained other endangered species, then it would be worthwhile.

4.4 C. Harvesting the population

The saddleback population on Mokoia Island, as well as other established island populations, can be used to provide birds for future reintroduction projects. In this final section, I explore the potential for harvesting the Mokoia Island population for future re-introduction projects.

This analysis is based on the concept of maximum sustainable yield. The concept originated with fisheries management in the 1950s (Newman, 1993). The maximum sustained yield is the point where the recruitment into the population matches the losses through harvesting and natural causes. As the reproductive success of the saddlebacks is negatively correlated with the population's density, harvesting the population will allow a higher growth rate because the population will be maintained at a lower level.

The maximum sustained yield is an unstable equilibrium. If more birds are removed than this, then the population will be rapidly driven towards extinction. Thus, it is not as simple as assessing the maximum number of birds that can be removed based on the population's birth and death rates. This would work if the population dynamics were deterministic, but with stochasticity it is unlikely that the numbers of birds in the population that can be removed can be easily calculated. Caughley and Sinclair (1994) recommend that the number of individuals removed should be 25% less than the maximum sustainable yield, as this would allow for variations in population size due to natural variation.

I have taken a different approach to estimate the maximum sustained yield by incorporating the effect of environmental variation into my estimate. By simulating the removal of birds using a stochastic model, I can estimate the number of birds that can be removed from the population without risking extinction.

4.4.1 Methods for simulating the harvesting of the population

The first part of this analysis was to estimate the largest number of birds that can be removed from the population without endangering the population, and the time that the population takes to recover to its previous size.

The second part looks at several different harvesting regimes (annual, biennial and triennial), to determine which scheme would allow more birds to be removed from the population, and the corresponding risk levels. I used a modified version of the model described in Chapter 3 to analyse the effects of removing large numbers of birds from the population.

All models began with 103 pairs, which was the average size of the population. The models then ran for five years, and the population was harvested in the sixth year. This allowed natural variation in the size of the population at the time of removal. The timing of the removal was at the end of the year, just before the breeding season, so no birds defined as juveniles were taken.

4.4.2 **Results**

The greatest number of birds that could be removed with one harvest without causing extinction was 139. The population took about 6 years to recover to its previous level after the removal of the birds (Figure 4.13).

Table 4.2. Maximum yields from the Mokoia Island saddleback population. The maximum number of birds that can be removed from the population is given for the three harvesting regimes (annual, biennial, and triennial), over periods of five years and 10 years. These results are given at three levels of extinction risk, 0%, 10 % and 20%. The numbers in brackets are the size of each harvest.

Harvesting regime	Length of harvesting scheme (years)	0% chance of extinction	10% chance of extinction	20% chance of extinction
Annual	5	355 (71)	405 (81)	430 (86)
	10	570 (57)	630 (63)	670 (67)
Biennial	5	384 (128)	435 (145)	459 (153)
	10	435 (87)	590 (118)	660 (132)
Triennial	5	278 (139)	324 (162)	342 (171)
	10	520 (130)	596 (149)	628 (157)

The regime that allows the greatest number of birds to be removed over five years is biennial harvesting (Table 4.2). When harvesting over five years the biennial scheme allows three harvests at, year one, year three, and year five. Over a ten-year period the annual harvesting scheme removes the greatest number of birds from the population. The maximum sustainable yield depends on how long the harvesting regime is maintained. Higher numbers of birds can be harvested if the time period is shorter (Figures 4.14). Annual harvesting has steeper extinction curves than the other two harvesting schemes.

Figure 4.13. Population recovery after one harvest of 139 birds (the highest number of birds that can be removed without creating an extinction risk). The removal occurs at year 2.

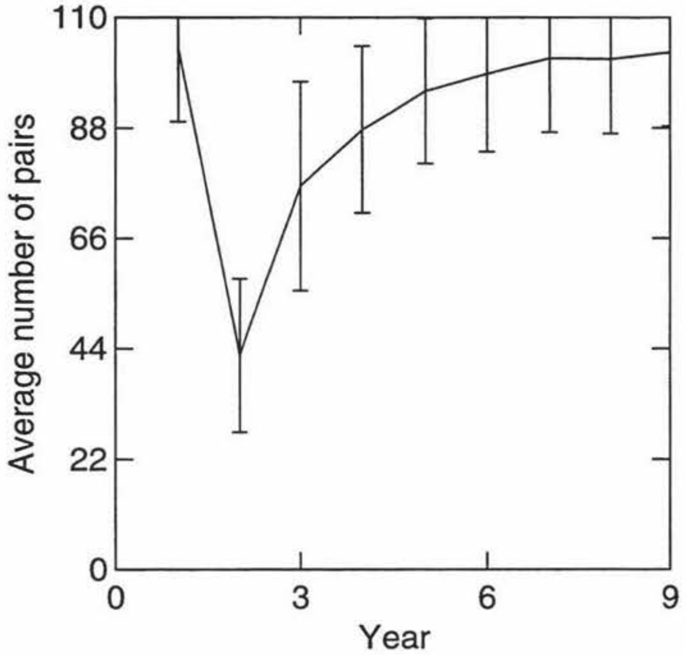
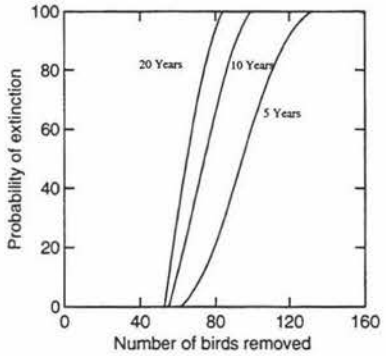
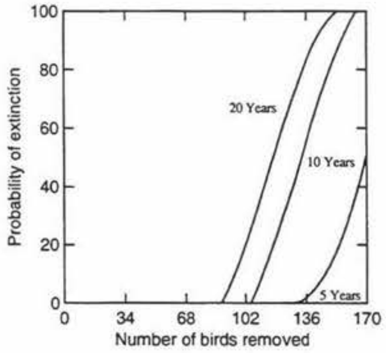


Figure 4.14. Extinction curves for population harvesting rates on an (A) annual, (B) biennial and (C) triennial basis. These regimes were conducted over 5, 10 and 20 year harvesting periods.

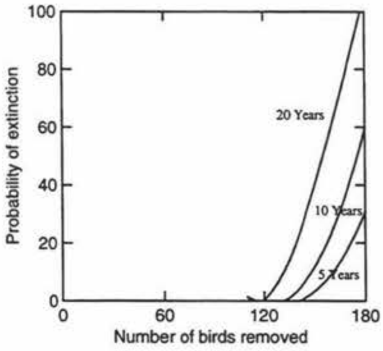
(A) Annual harvesting



(B) Biennial



(C) Triennial



4.4.3 Discussion

These models show that the high population growth rate at low densities allows up to half the population to be removed in a single event without a significant risk of the population going extinct. This is not surprising, as the analysis of the population demographics showed that at low population levels there was a high recruitment rate of fledglings into the population. One point of note is that the highest number of birds that can be removed from the population is 139, which is the same as the number of birds that can be removed from the population triennially (for a five year period). While it takes the population six years to recover to its previous level, it has recovered enough in three years to allow a second removal of 139 birds. However, the results for the ten-year period show that the number of birds removable at a single harvest is reduced.

Continuous harvesting would artificially maintain the population at low population levels, as the population suffers higher "mortality" than it would normally. This could potentially increase the population's vulnerability to catastrophes. The models that I used here have not included the effect of catastrophes (extremes of environmental variation), as the results from these events are fairly idiosyncratic (Simberloff, 1988). In the aftermath of a catastrophe the species is likely to require additional management. Without knowing what the catastrophe is, or how severe, then this is difficult to incorporate into a model. However, if the species is sustaining high "mortality" at the time through harvesting, then the effects may be even more severe because of the lower population levels.

This analysis has shown that island populations can be harvested continuously at low risk. This creates a "surplus" of individuals that could be used to establish additional populations. As the populations can be harvested readily without risk, it would be acceptable to attempt mainland reintroductions to managed regions to see if a sustainable population can be established.

If a mainland population were to be established in an area where it is almost self-sustaining (with predator control) then island populations can be harvested to provide additional birds to increase the mainland population's viability. This would be an artificial version of the rescue effect of metapopulation dynamics (Brown and Kodric-Brown, 1977), where populations are "rescued" from extinction by dispersal from other populations. The mainland would effectively be a sink (Pulliam, 1988; Pulliam and Danielson, 1991), with the island populations acting as sources. Dias (1996) discussed several types of source sink dynamics, where the quality of the sink was the defining factor. If the sink was just poorer quality habitat, then dispersal would maintain it at a higher population density than the population itself would achieve. However, there can be "black hole" sinks where the individuals disappear through high mortality. It seems likely that most of the mainland will effectively be black hole sinks due to exotic predators. However, with predator control, and population supplementation, it may be possible to produce a sustainable population on the mainland.

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Appendix A

General Linear Models fitted to the reproductive data

This appendix lists the models that were fitted to the reproductive data using SYSTAT 6.0. The ANOVA tables list the terms and interactions fitted in individual models.

The variables fitted were:

DENSITY	The number of pairs in the population.
MAL_AGE	The age of the male.
FEM_AGE	The age of the female.
FEMAGEK$	The age class of the female. There were two age classes, first year and second year and older.
MALEAGEK$	The age class of the male. There were two age classes, first year and second year and older.
PAIR$	This fitted a separate term for each pair.
NO_YR$	The number of years that a pair has been together.
LOCATION$	The quarter of the island that the birds were nesting in.
FLS	The number of fledglings produced.
MALE$	This fits a seperate term for each male bird.
FEMALE$	This fits a seperate term for each female bird.
BOXUSE	The proportion of nesting attempts per year that were in nest boxes for each female.
BOXUSE2	This term was the porportion of nestbox use from all data records for a particular female.

The $ indicates categorical variables. Some of the models included interactions between various terms. These are indicated by VARIABLE*VARIABLE. The models are listed in order of increasing R^2.

Model 1

Dep Var: FLS N: 145 Multiple R: 0.6508 Squared multiple R: **0.4235**

Analysis of Variance

Source	Sum-of-Squares	DF	Mean-Square	F-Ratio	P
FEMAGEK$	52.9868	1	52.9868	24.7935	0.0000
MALEAGEK$	22.7163	1	22.7163	10.6293	0.0014
DENSITY	15.1689	1	15.1689	7.0978	0.0086
Error	301.3351	141	2.1371		

Model 2

Dep Var: FLS N: 124 Multiple R: 0.6629 Squared multiple R: **0.4394**

Analysis of Variance

Source	Sum-of-Squares	DF	Mean-Square	F-Ratio	P
DENSITY	4.7094	1	4.7094	2.6706	0.1050
BOXUSE	52.0534	5	10.4107	5.9036	0.0001
FEMAGEK$	13.7651	1	13.7651	7.8058	0.0061
MALEAGEK$	11.4217	1	11.4217	6.4770	0.0123
Error	202.7953	115	1.7634		

Model 3

Dep Var: FLS N: 145 Multiple R: 0.6668 Squared multiple R: **0.4446**

Analysis of Variance

Source	Sum-of-Squares	DF	Mean-Square	F-Ratio	P
DENSITY	15.0510	1	15.0510	7.1541	0.0084
FEMAGEK$	49.2352	1	49.2352	23.4028	0.0000
MALEAGEK$	21.1724	1	21.1724	10.0638	0.0019
LOCATION$	11.0084	3	3.6695	1.7442	0.1608
Error	290.3268	138	2.1038		

Model 4

Dep Var: FLS N: 145 Multiple R: 0.6747 Squared multiple R: **0.4552**

Analysis of Variance

Source	Sum-of-Squares	DF	Mean-Square	F-Ratio	P
FEMAGEK$	24.0557	1	24.0557	11.5722	0.0009
MALEAGEK$	17.9219	1	17.9219	8.6215	0.0039
DENSITY	24.3542	1	24.3542	11.7158	0.0008
NO_YR$	16.5472	4	4.1368	1.9900	0.0994
Error	284.7880	137	2.0787		

Model 5

Dep Var: FLS N: 145 Multiple R: 0.6878 Squared multiple R: **0.4730**

Analysis of Variance

Source	Sum-of-Squares	DF	Mean-Square	F-Ratio	P
DENSITY	23.8448	1	23.8448	11.5997	0.0009
MALEAGEK$	17.0568	1	17.0568	8.2976	0.0046
FEMAGEK$	21.9869	1	21.9869	10.6959	0.0014
LOCATION$	9.3328	3	3.1109	1.5134	0.2140
NO_YR$	14.8716	4	3.7179	1.8086	0.1308
Error	275.4552	134	2.0556		

Model 6

Dep Var: FLS N: 133 Multiple R: 0.8899 Squared multiple R: **0.7919**

Analysis of Variance

Source	Sum-of-Squares	DF	Mean-Square	F-Ratio	P
DENSITY	3.6013	1	3.6013	2.4552	0.1222
BOXUSE2	0.1428	1	0.1428	0.0974	0.7560
PAIR$	345.4808	68	5.0806	3.4637	0.0000
Error	90.9420	62	1.4668		

Model 7

Dep Var: FLS N: 124 Multiple R: 0.9133 Squared multiple R: **0.8341**

Analysis of Variance

Source	Sum-of-Squares	DF	Mean-Square	F-Ratio	P
DENSITY	1.0631	1	1.0631	0.9389	0.3370
PAIR$	299.3088	68	4.4016	3.8875	0.0000
BOXUSE	0.0009	1	0.0009	0.0008	0.9781
Error	60.0097	53	1.1323		

Model 8

Dep Var: FLS N: 145 Multiple R: 0.9449 Squared multiple **R: 0.8929**

Analysis of Variance

Source	Sum-of-Squares	DF	Mean-Square	F-Ratio	P
DENSITY	2.3993	1	2.3993	2.6140	0.1111
MALEAGEK$	34.9540	1	34.9540	38.0831	0.0000
PAIR$	298.3340	81	3.6831	4.0129	0.0000
Error	55.9880	61	0.9178		

Model 9

Dep Var: FLS N: 145 Multiple R: 0.9204 Squared multiple R: **0.8472**

Analysis of Variance

Source	Sum-of-Squares	DF	Mean-Square	F-Ratio	P
DENSITY	6.9917	1	6.9917	6.3019	0.0143
MALEAGEK$	6.2025	1	6.2025	5.5905	0.0208
FEMAGEK$	18.7567	1	18.7567	16.9061	0.0001
FEMALE$	221.4538	69	3.2095	2.8928	0.0000
Error	79.8814	72	1.1095		

Model 10

Dep Var: FLS N: 145 Multiple R: 0.9363 Squared multiple R: **0.8767**

Analysis of Variance

Source	Sum-of-Squares	DF	Mean-Square	F-Ratio	P
DENSITY	8.7989	1	8.7989	9.6909	0.0027
MALE$	236.8703	70	3.3839	3.7269	0.0000
MALEAGEK$	9.7827	1	9.7827	10.7744	0.0016
FEMAGEK$	14.2708	1	14.2708	15.7176	0.0002
Error	64.4648	71	0.9080		

Model 11

Dep Var: FLS N: 145 Multiple R: 0.9469 Squared multiple R: **0.8967**

Analysis of Variance

Source	Sum-of-Squares	DF	Mean-Square	F-Ratio	P
DENSITY	3.9999	1	3.9999	4.5172	0.0376
FEMAGEK$	36.9280	1	36.9280	41.7042	0.0000
PAIR$	270.0375	81	3.3338	3.7650	0.0000
Error	54.0139	61	0.8855		

Model 12

Dep Var: FLS N: 145 Multiple R: 0.9469 Squared multiple R: **0.8967**

Analysis of Variance

Source	Sum-of-Squares	DF	Mean-Square	F-Ratio	P
DENSITY	3.9999	1	3.9999	4.5172	0.0376
PAIR$	270.0375	81	3.3338	3.7650	0.0000
FEMAGEK$	36.9280	1	36.9280	41.7042	0.0000
Error	54.0139	61	0.8855		

Model 13

Dep Var: FLS N: 145 Multiple R: 0.9525 Squared multiple R: **0.9072**

Analysis of Variance

Source	Sum-of-Squares	DF	Mean-Square	F-Ratio	P
DENSITY	5.3962	1	5.3962	6.6725	0.0122
FEMAGEK$	7.4643	1	7.4643	9.2297	0.0035
MALEAGEK$	5.4903	1	5.4903	6.7888	0.0116
LOCATION$	1.1658	3	0.3886	0.4805	0.6971
PAIR$	241.8031	78	3.1000	3.8332	0.0000
Error	48.5236	60	0.8087		

Model 14

Dep Var: FLS N: 145 Multiple R: 0.9525 Squared multiple R: **0.9072**

Analysis of Variance

Source	Sum-of-Squares	DF	Mean-Square	F-Ratio	P
MALE$	109.4742	46	2.3799	2.9427	0.0001
FEMALE$	78.9186	35	2.2548	2.7881	0.0002
DENSITY	5.3962	1	5.3962	6.6725	0.0122
MALEAGEK$	5.4903	1	5.4903	6.7888	0.0116
FEMAGEK$	7.4643	1	7.4643	9.2297	0.0035
Error	48.5236	60	0.8087		

Model 15

Dep Var: FLS N: 145 Multiple R: 0.9525 Squared multiple R: **0.9072**

Analysis of Variance

Source	Sum-of-Squares	DF	Mean-Square	F-Ratio	P
FEMAGEK$	7.4643	1	7.4643	9.2297	0.0035
MALEAGEK$	5.4903	1	5.4903	6.7888	0.0116
DENSITY	5.3962	1	5.3962	6.6725	0.0122
PAIR$	252.8115	81	3.1211	3.8593	0.0000
Error	48.5236	60	0.8087		

Model 16

Dep Var: FLS N: 145 Multiple R: 0.952476 Squared multiple R: **0.9072**

Analysis of Variance

Source	Sum-of-Squares	DF	Mean-Square	F-Ratio	P
MALEAGEK$	2.074467	1	2.074467	2.523420	0.117512
FEMAGEK$	7.484714	1	7.484714	9.104547	0.003760
PAIR$	248.8426	81	3.072131	3.736998	0.000000
DENSITY	2.733649	1	2.733649	3.325263	0.073290
DENSITY*MALEAGEK$	0.020592	1	0.020592	0.025049	0.874786
Error	48.503032	59	0.822085		

Model 17

Dep Var: FLS N: 145 Multiple R: 0.952533 Squared multiple R: **0.9073**

Analysis of Variance

Source	Sum-of-Squares	DF	Mean-Square	F-Ratio	P
DENSITY	5.2105	1	5.2105	6.3455	0.0144
MALEAGEK$	3.2731	1	3.2731	3.9862	0.0504
FEMAGEK$	5.0307	1	5.0307	6.1266	0.0162
PAIR$	251.9891	81	3.1109	3.7885	0.0000
MALEAGEK$*FEMAGEK$	0.0769	1	0.0769	0.0936	0.7606
Error	48.4467	59	0.8211		

Model 18

Dep Var: FLS N: 145 Multiple R: 0.9540 Squared multiple R: **0.9100**

Analysis of Variance

Source	Sum-of-Squares	DF	Mean-Square	F-Ratio	P
DENSITY	1.2635	1	1.2635	1.5046	0.2251
MALEAGEK$	4.8860	1	4.8860	5.8184	0.0192
FEMAGEK$	2.4746	1	2.4746	2.9468	0.0916
LOCATION$	1.5071	3	0.5024	0.5982	0.6188
NO_YR$	1.4980	4	0.3745	0.4460	0.7748
PAIR$	228.4296	78	2.9286	3.4875	0.0000
Error	47.0256	56	0.8397		

Model 19

Dep Var: FLS N: 145 Multiple R: 0.9540 Squared multiple R: **0.9100**

Analysis of Variance

Source	Sum-of-Squares	DF	Mean-Square	F-Ratio	P
FEMAGEK$	2.4746	1	2.4746	2.9468	0.0916
MALEAGEK$	4.8860	1	4.8860	5.8184	0.0192
DENSITY	1.2635	1	1.2635	1.5046	0.2251
NO_YR$	1.4980	4	0.3745	0.4460	0.7748
PAIR$	237.7624	81	2.9353	3.4955	0.0000
Error	47.0256	56	0.8397		

Model 20

Dep Var: FLS N: 124 Multiple R: 0.9541 Squared multiple R: **0.9103**

Analysis of Variance

Source	Sum-of-Squares	DF	Mean-Square	F-Ratio	P
DENSITY	3.8280	1	3.8280	6.0184	0.0176
BOXUSE	0.1083	1	0.1083	0.1703	0.6816
FEMAGEK$	0.8674	1	0.8674	1.3638	0.2483
MALEAGEK$	10.3059	1	10.3059	16.2031	0.0002
PAIR$	221.6069	68	3.2589	5.1237	0.0000
Error	32.4383	51	0.6360		

Model 21

Dep Var: FLS N: 145 Multiple R: 0.954214 Squared multiple R: **0.9105**

Analysis of Variance

Source	Sum-of-Squares	DF	Mean-Square	F-Ratio	P
MALEAGEK$	5.7598	1	5.759860	7.2659	0.0091
FEMAGEK$	0.23201	1	232033	0.2927	0.5905
PAIR$	253.981	81	3.135673	3.9555	0.0000
DENSITY	7.1485	1	7.148551	9.0177	0.0039
DENSITY*FEMAGEK$	1.7529	1	1.752978	2.2113	0.1423
Error	46.7706	59	0.7927		

Model 22

Dep Var: FLS N: 145 Multiple R: 0.9693 Squared multiple R: **0.9394**

Analysis of Variance

Source	Sum-of-Squares	DF	Mean-Square	F-Ratio	P
DENSITY	0.0315	1	0.0315	0.0428	0.8371
PAIR$	182.5990	81	2.2825	3.1009	0.0001
MAL_AGE$	17.9863	7	1.9985	2.7150	0.0134
FEM_AGE$	19.7734	7	1.7976	2.4421	0.0182
Error	31.6515	49	0.7361		

The best fitting model is Model 17, even though four models (17-22 have higher R^2 values than it. The higher fitting models include variables that are not significant, which explain low proportions of the variance in the data. When these models are simplified by removing them, the fit worsens.

Appendix B

Program Listing

B.1 Mokoia Island Saddleback Population Model

This is the basic saddleback population model developed in Chapter 3. It is written in the C++ programming language, and is broken down into various functions to accomplish tasks, such as survival and reproduction.

```
// new version started 2 dec 98

#include <iostream.h>
#include <stdlib.h>
#include <math.h>
#include <time.h>

// declaration of global variables

double evse = 0.057;           // S.D. for environmental stochasticity in adult survival.
double evjse = 0.056;          // S.D. for environmental stochasticity in juvenile survival.
double evbse = 0.2020;         // S.D. for environmental stochasticity in reproduction.
double juvemort = 4.441;
double ddmort = -0.03254;
double ddbirth = -0.01688;
double admort = 4.693;
double pqsd = 1.264;
double male2 = 0.3540;
double male1 = -0.3540;
double female2 = 1.0468;
double female1 = -1.0468;
double birthint =3.2280;
double sexratio = 0.41;

int main (void)
{
// functions called
double sort1 (int* pm, int* pf, double* pq, int* pairs, int* umc, int* ufc, int* um, int* uf);
int sort2 (int* array, int* count);
int juvesexing (int* juv, int* um, int* uf, int* umc, int* ufc);
int age (int* array, int* count);
int pairings (int* um, int* uf, int* umc, int* ufc, int* pm, int* pf, int* pair, double* pq);
double normrand (void);
int reproduction (int* pm, int* pf, double* pq, int* pair, int* juv, double* evbi);
int adultmortality (int* array, int* count, double* ev);
int juvenilemortality (int* count,int* count2, double* evad, double* evju);
double pairquality (void);
double stats (int* avpair, int* avufc, int* avumc, int* avextinct,int* exc);

randomize();
// array definition
int pairedmales [600] = {0};
```

```
int pairedfemales [600] = {0};
double pairqualit [600] = {0};
int unpairedmales [600] = {0};
int unpairedfemales [600] = {0};
int avepair [1005] = {0};
int aveumc [1005] = {0};
int aveufc [1005] = {0};
int aveextinct [1005] = {0};

// definition of pointers to arrays
int *pm;
pm = pairedmales;
int *pf;
pf = pairedfemales;
double *pq;
pq = pairqualit;
int *um;
um = unpairedmales;
int *uf;
uf = unpairedfemales;
int *avpair;
avpair = avepair;
int *avumc;
avumc = aveumc;
int *avufc;
avufc = aveufc;
int *avextinct;
avextinct = aveextinct;

// definition of variables
int juve = 0;                    // juveniles kept count just as a variable
int paircount = 0;               // number of pairs
int numunmales = 0;              // number of unpaired males
int numunfemales = 0;            // number of unpaired females
// pointers to these variables
int *juv;
int *umc;
int *pair;
int *ufc;

pair = &paircount;
umc = &numunmales;
ufc = &numunfemales;
juv = &juve;

// misc variables
const  double pi = 3.14159;
int year;
int a;
double vara, varb;
int q;
double environmentalvariationadult;
double environmentalvariationjuven;
double environmentalvariationbirth;
double* evbi;
double* evad;
double* evju;
evad = &environmentalvariationadult;
evju = &environmentalvariationjuven;
```

```
evbi = &environmentalvariationbirth;
int simulation = 0;
int excount = 0;                // number of times population goes extinct
int *exc;
exc = &excount;
double env = 0;

for (simulation = 0; simulation <1000; simulation++)
  {
  cout<<simulation<<endl;
  avepair [simulation] = paircount;
  aveumc [simulation] = numunmales;
  aveufc [simulation] = numunfemales;
  for (a = 15; a < 400; a++)
       {
       pairedmales [a] = 0;
       pairedfemales [a] = 0;
       pairqualit [a] = 0;
       unpairedfemales [a] = 0;
       unpairedmales [a] = 0;
       }
  numunfemales = 0;
  numunmales = 0;
  // initialising arrays with 15 pairs
  for(a = 0; a < 15; a++)
       {
       pairedmales [a] = ( random(4)) + 1;
       pairedfemales [a] = (random(4)) +1;
       vara = (double (random(1001))) / 1000 ;
       varb = (double (random(1001))) / 1000;
       if (vara == 0) (vara = 0.001);
       pairqualit [a] =pqsd * ((sqrt (-2 * log(vara))) * (cos(2 * pi * varb)));
       }
  paircount = 15;

  for (year = 0; year < 50; year++)
       {
       env = normrand();               // producing value for environmental stochasticity
       *(evad) = env * evse;
       *(evju) = env * evjse;
       *(evbi) = env * evbse;
       reproduction (pm, pf, pq, pair, juv, evbi);
       adultmortality (pm, pair, evad);
       adultmortality (pf, pair, evad);
       adultmortality (um, umc, evad);
       adultmortality (uf, ufc, evad);
       juvenilemortality (juv, pair, evad, evju);
       sort2 (um, umc);
       sort2 (uf, ufc);
       sort1 (pm, pf, pq, pair, umc, ufc, um, uf);
       age (pm, pair);          // age paired males
       age (pf, pair);          // age paired females
       age (um, umc);
       age (uf, ufc);
       juvesexing (juv, um, uf, umc, ufc);
       pairings (um, uf, umc, ufc, pm, pf, pair, pq);

       if (*(pair) == 0 && *(ufc) == 0) {
              aveextinct [excount] = year;
```

```
                excount++;
                year = 51;
                }
        else if (*(pair) == 0 && *(umc) == 0) {
                aveextinct [excount] = year;
                excount++;
                year = 51;
                }

        }
   }
stats (avpair, avufc, avumc, avextinct, exc);
cout<<"finished"<<"maybe"<<endl;

return(0);
}


// function listings

double stats (int* avpair, int* avufc, int* avumc, int* avextinct, int* exc)
        {
        // stats variables.
        long int apair = 0;
        long int aufc = 0;
        long int aumc = 0;
        long int atex = 0;
        long int ex = *(exc);
        double apairsd = 0;
        double aufcsd = 0;
        double aumcsd = 0;
        double atexsd = 0;
        int q = 0;
        for (q = 1; q< 1001; q++)
                {
                apair = apair + *(avpair + q);
                aufc = aufc + *(avufc + q);
                aumc = aumc + *(avumc + q);
                atex = atex + *(avextinct + q);
                }
        for (q = 1; q<1001; q++)
                {
                apairsd = apairsd + pow((*(avpair+q) - (apair/1000)),2);
                aufcsd = aufcsd + pow((*(avufc+q) - (aufc/1000)),2);
                aumcsd = aumcsd + pow((*(avumc+q) - (aumc/1000)),2);
                }
        for (q = 0; q < ex; q++)
                {
                atexsd = atexsd + pow((*(avextinct+q) - (atex/ex)),2);
                }
        cout<<"average # of pairs :"<<double (apair)/1000<<endl;
        cout<<"s.d. of pair :"<<sqrt(apairsd /1000)<<endl;
        cout<<"average # of unpaired males :"<<(double (aumc))/1000<<endl;
        cout<<"s.d. of unpaired males :"<<sqrt(aumcsd /1000)<<endl;
        cout<<"average # of unpaired females :"<<(double (aufc))/1000<<endl;
        cout<<"s.d. of unpairedfemales :"<<sqrt(aufcsd /1000)<<endl;
        cout<<"# of times extinct :"<<*(exc)<<endl;
        if (*(exc) > 0)
                {
```

```
                cout<<"s.d. of # times extinct :"<<sqrt(atexsd/ex)<<endl;
                cout<<"average # of years to extinction :"<<double (atex/ex)<<endl;
                }
        return(0);
        }

double sort1 (int* pm, int* pf, double* pq, int* pair, int* umc, int* ufc, int* um, int* uf)
        {
        // This function sorts throughout the paired arrays removing those
        // individuals that are zero values and moving their partners into
        // the unpaired arrays.
        int q = 0;
        int i = 0;
        int p = *(pair);
        int male = *(umc);
        int female = *(ufc);
        int ma [400] = {0};
        int fe [400] = {0};
        double pqb [400] = {0};
        for (q = 0; q < p; q++)
                {
                if ((*(pm + q) == 0) && (*(pf + q) > 0))
                        {
                        *(uf + female) = *(pf + q);
                        *(pf + q) = 0;
                        female++;
                        }
                if ((*(pf + q) == 0) && (*(pm + q) > 0))
                        {
                        *(um + male) = *(pm + q);
                        *(pm + q) = 0;
                        male++;
                        }
                if ((*(pf + q) > 0) && (*(pm + q) > 0))
                        {
                        ma [i] = *(pm + q);
                        fe [i] = *(pf + q);
                        pqb [i] = *(pq + q);
                        i++;
                        *(pm + q) = 0;
                        *(pf + q) = 0;
                        *(pq + q) = 0;
                        }
                }
        for (q = 0; q < i; q++)
                {
                *(pm + q) = ma[q];
                *(pf + q) = fe[q];
                *(pq + q) = pqb[q];
                }
        *(pair) = i;
        *(umc) = male;
        *(ufc) = female;
        return(0);
        }


int sort2 (int* array, int* count)
        {
```

```
        // this function sorts the array removing those individuals that are
        // now zero values.  This is done for the two arrays for unpaired
        // males and females.
        int secondarray [400] = {0};
        int q;
        int i = 0;
        int p = *(count);
        for (q = 0; q< p; q++)
                {
                if (*(array + q) > 0)
                        {
                        secondarray [i] = *(array + q);
                        i++;
                        *(array + q) = 0;
                        }
                }
        for (q=0; q< i; q++)
                {
                *(array + q) = secondarray [q];
                }
        *(count) = i;
        return(0);
        }

int juvesexing (int* juv, int* um, int* uf, int* umc, int* ufc)
        {
        // function to assign sex to surviving juveniles.
        int q;
        double var;
        int mc;
        // male count
        int fc;
        // female count
        int jc;
        mc = *(umc);
        fc = *(ufc);
        jc = *(juv);
        for (q=0; q< jc; q++)
                {
                var = double( random(1001)) / 1000;
                if (var > sexratio)
                        {
                        *(um + mc) = 1;
                        mc++;
                        }
                else
                        {
                        *(uf + fc) = 1;
                        fc++;
                        }
                }
        *(juv) = 0;
        *(umc) = mc;
        *(ufc) = fc;
        return(0);
                }

int age (int* array, int* count)
        {
```

```
        // goes through each array and increments all values by one
        // except zero values
        int q;
        int p;
        p = *(count);
        for (q=0; q< p; q++)
                {
                *(array + q) = *(array + q) + 1;
                }
        return(0);
        }

int pairings (int* um, int* uf, int* umc, int* ufc, int* pm, int* pf, int* pair, double* pq)
        {
        int morefemales (int* um, int* uf, int* umc, int* ufc, int* pm, int* pf, int* pair, double* pq);
        int moremales (int* um, int* uf, int* umc, int* ufc, int* pm, int* pf, int* pair, double* pq);
        // function to create pairs
        if (*(ufc) > *(umc) && *(umc) > 0) (morefemales(um, uf, umc, ufc, pm, pf, pair, pq));
        else
        {
        if (*(ufc) > 0 && *(umc) > 0)
        (moremales(um, uf, umc, ufc, pm, pf, pair, pq));
        }
        return(0);
        }

int morefemales (int* um, int* uf, int* umc, int* ufc, int* pm, int* pf, int* pair, double* pq)
        {
        // works through unpaired female array.
        double pairquality ();
        int q;
        int k = *(pair);
        int p = *(umc);
        int r = 0;
        if (p > 0) {
        for (q = 0; q < p; q++)
                {
                *(pf + k) = *(uf + r);
                *(pm + k) = *(um + q);
                *(pq + k) = pairquality();
                *(um + q) = 0;
                *(uf + r) = 0;
                k++;
                r++;
                }
        *(umc) = 0;
        *(pair) = k;
        sort2 (uf, ufc);

        }
        return(0);
        }

int moremales (int* um, int* uf, int* umc, int* ufc, int* pm, int* pf, int* pair, double* pq)
        {
        // Works  through unpaired male array.
        double pairquality ();
        int q;
        int k = *(pair);
```

```
        int p = *(ufc);
        int r = 0;
        if (p > 0){
        for (q = 0; q < p; q++)
                {
                *(pf + k) = *(uf + q);
                *(pm + k) = *(um + r);
                *(pq + k) = pairquality();
                *(um + r) = 0;
                *(uf + q) = 0;
                k++;
                r++;
                }
        *(ufc) = 0;
        sort2 (um, umc);
        *(pair) = k;
        }
        return(0);
        }

double pairquality (void)
        {
        double normrand (void);
        double pairqualityb;
        pairqualityb = (normrand() * pqsd);
        return(pairqualityb);
        }

int reproduction (int* pm, int* pf, double* pq, int* pair, int* juv, double* evbi)
        {
        double normrand (void);
        // function to calculate number of juveniles produced
        int q;
        int p;
        double fledglings = 0;
        double fledgling = 0;
        double  magek;
        double  fagek;
        double  dd;
        double evb;
        p = *(pair);
        dd = (ddbirth) * p ;
        if (dd > 0) (dd = 0);
        for (q = 0; q< p; q++)
                {
                if (*(pm+q) == 1) (magek = male1);
                else (magek = male2);
                if (*(pf+q) == 1) (fagek = female1);
                else (fagek = female2);
                evb = normrand() * 0.71605;
                fledgling =( magek + fagek + *(pq+q) + dd + *(evbi) +  birthint + evb);
                if ((int(fledgling) - fledgling) < -0.5) (fledgling = int(fledgling) +1);
                else (fledgling = int(fledgling));
                if (fledgling < 0 ) (fledgling = 0);
                fledglings = fledglings + fledgling;
                }
        *(juv) = int (fledglings);
        return(0);
        }
```

```
double normrand (void)
        {
        // creates a random number which is normally distributed with a
        // mean of 0 and a s.d. of 1
        double var3;
        double var1, var2;
        const  double pi = 3.14159;
        var1 = (double (random(10001))) / 10000 ;
        var2 = (double (random(10001))) / 10000;
        if (var1 == 0) (var1 = 0.001);
        var3 = ((sqrt (-2 * log(var1))) * (cos(2 * pi * var2)));
        return(var3);
        }

int adultmortality (int* array, int* count, double* evad)
        {
        //    function to calculate mortality
        int q = 0;
        int p = *(count);
        int i = 0;
        double reapersprob = 0;
        double var2 = 0;
        double reapersprob2 = 0;
        double mort = exp (admort);
        reapersprob = mort / (1+ mort);
        reapersprob2 = (pow(reapersprob, 12)) + *(evad);
        for (q = 0; q < p; q++)
                {
                var2 = (double( random(10001))) / 10000;
                if (var2 > reapersprob2) (*(array + q) = 0, i++);
                if (*(array + q) > 30) (*(array + q) = 0);
                }
        return(0);
        }

int juvenilemortality (int* juv,int* pair, double* evad, double* evju)
        {
        // function to deal to juveniles
        int q = 0;
        double var5 = 0;
        double reapersprob1 = 0;              // linear part of logit
        double reapersprob2 = 0;              // first nine months (Juvenile survival)
        double reapersprob3 = 0;              // final three months (adult survival)
        double reapersprob4 = 0;              // :-)
        double mort = 0;
        double mort2 = 0;
        int deathscount = 0;
        double dd = 0;
        int p = *(juv);
        if (p >0) {
        mort =exp (admort);
        dd = *(pair) * (ddmort);
        if (dd >0) (dd = 0);
        mort2 = exp(juvemort + dd);

        reapersprob1 =  mort2 / (1 + mort2);
        reapersprob2 = pow(reapersprob1,9);                 //Juvenile survival, first3/4 of year
        reapersprob3 = pow((mort / (1 + mort)), 3);         // survival for remaining 1/4 year
```

```
        reapersprob4 = (reapersprob2 * reapersprob3) + *(evju); // complete survival            probability

        for (q = 0; q < p; q++)
                {
                var5 = (double( random(10001))) / 10000;
                if (var5 > reapersprob4) (deathscount++);
                }
          }
        *(juv) = p - deathscount;
        return(0);
        }


// end of listing
```

To calculate the rate of growth the statisitics function was replaced with the following code, which was placed within the main function of the program.

```
int p = 0;
double avepairr = 0;
double avpairsd = 0;
double ave[5] = {0};
double std[5] = {0};

        avepairr = 0;
        avpairsd = 0;

for (p=0; p<200; p++)
                {
                avepairr  = avepairr + (avepairyear[0][p]/ 15);
                }
for (p=0; p<200; p++)
     {
     avpairsd = avpairsd + pow (((avepairyear[0][p] / 15) - (avepairr/200)),2);
     }

ave [0] = avepairr/200;
std [0] = avpairsd;


for (q = 1;q<4; q++)
        {
        avepairr = 0;
        for (p=0; p<200; p++)
                {
                avepairr  = avepairr + (avepairyear[q][p]/ avepairyear[q-1][p]);
                }
        ave [q] = avepairr/200;
        }
double aveb = 0;
for (q=0; q<4; q++)
        {
        aveb = ave[q] + aveb;
        }


for (p=0; p<200; p++)
        {
```

```
        for (q = 1;q<4; q++)
                {
                avpairsd = avpairsd + pow (((avepairyear[q][p] / avepairyear[q-1][p]) - (aveb/4)),2);
                }
        }

cout<<"ave r = "<<aveb/4<<" std dev = "<<sqrt(avpairsd/800)<<endl;
cout<<"finished"<<"maybe"<<endl;
```

B.2. Sensitivity analysis

To run the sensitivity analysis I added a series of statements which altered the parameters by a some number of standard errors from the estimated value.

```
double stdder = 0;                    // number of s.e.'s to alter parameters estimate.
cout<<"input sex ratio :";
cin>>stdder;

//juvemort = 4.441 + (0.4272 * stdder);
//ddmort = -0.03257 + (0.006925 * stdder);
//ddbirth = -0.0169 + (0.00779 * stdder);
//admort = 4.693 + (0.2240 * stdder) ;
//birthint = 3.2280 + (0.4224 * stdder);
//male2 = male2 + (stdder * 0.2720 );
//male1 = male1 - (stdder * 0.2720);
//female2 = female2 + (stdder * 0.2720);
//female1 = female1 - (stdder * 0.2720);
//pqsd = pqsd * stdder;
sexratio = sexratio + (stdder * 0.018);
//maxage = stdder;
```

There were multiple programs produced, with selected parameters altered. This example alters the sex ratio only for the population (the other values have been commented out by using the //).

B.3. Modified mortality routines with poison drop included

To include the effect of the poison in the model two additional functions were created to calculate survival in that year. The code calling the survival functions was altered so that in the designated year, the altered functions would be called. This is given below:

```
if (year != poisonyear){
        adultmortality (pm, pair, evad, year);
        adultmortality (pf, pair, evad, year);
        adultmortality (um, umc, evad, year);
        adultmortality (uf, ufc, evad, year);
        juvenilemortality (juv, pair, evad, evju);
        sort2 (um, umc);
        sort2 (uf, ufc);
```

```
        sort1 (pm, pf, pq, pair, umc, ufc, um, uf);
        }

        if (year == poisonyear) {
        poisonadultmortality (pm, pair, evad);
        poisonadultmortality (pf, pair, evad);
        poisonadultmortality (um, umc, evad);
        poisonadultmortality (uf, ufc, evad);
        poisonjuvenilemortality (juv, pair, evad, evju);
        sort2 (um, umc);
        sort2 (uf, ufc);
        sort1 (pm, pf, pq, pair, umc, ufc, um, uf);
```

The listings for the survival fucntions that simulated the effect of the poison drop (one affecting juveniles, the other adults) is given below. Poisad is the value for the effect of the poison.

```
int poisonadultmortality (int* array, int* count, double* evad)
        {
        //      function to calculate mortality
        int q = 0;
        int p = *(count);
        int i = 0;
        double reapersprob = 0;
        double var2 = 0;
        double reapersprob2 = 0;
        double reapersprob1 = 0;
        double mort2 = 0;
        double mort = exp (admort );
        reapersprob = mort / (1+ mort);
        mort2 = exp (admort + poisad );
        reapersprob1 = mort2 / (mort2 + 1);
        reapersprob2 = (pow(reapersprob, 11) * reapersprob1) + *(evad);

        for (q = 0; q < p; q++)
                {
                var2 = (double( random(10001))) / 10000;
                if (var2 > reapersprob2) (*(array + q) = 0, i++);
                if (*(array + q) > 30) (*(array + q) = 0);
                }
                return(0);
        }

int poisonjuvenilemortality (int* juv,int* pair, double* evad, double* evju)
        {
        // function to deal to juveniles
        int q = 0;
        double var5 = 0;
        double reapersprob1 = 0;
        double reapersprob2 = 0;        // first nine months
        double reapersprob3 = 0;        // final three months (adult survival)
        double reapersprob4 = 0;        // :-)
        double reapersprob5 = 0;
        double mort = 0;
        double mort2 = 0;
        double mort1 = 0;
```

```
int deathscount = 0;
double dd = 0;
int p = *(juv);
if (p >0) {
mort =exp (admort);
dd = *(pair) * (ddmort);
mort2 = exp(juvemort + dd);

reapersprob1 =  mort2 / (1 + mort2);
reapersprob2 = pow(reapersprob1,9);
reapersprob3 = pow((mort / (1 + mort)), 2);
mort1 = exp (admort + poisad);
reapersprob5 = mort1 / (mort1 + 1);
reapersprob4 = (reapersprob2 * reapersprob3 * reapersprob5) + *(evju);

        for (q = 0; q < p; q++)
        {
        var5 = (double( random(10001))) / 10000;
        if (var5 > reapersprob4) (deathscount++);
        }
  }
*(juv) = p - deathscount;
return(0);
}
```

B.4 Routines for harvesting the population.

Below is the program listing for the routine which removed birds from the population to simulate harvesting.

```
int removal (int * array1, int* array2,int* count1, int* array3,int* count2, int* array4, int* count3, int
numbirds)
//routine for selecting birds for transfer.
// will move selected number of birds out of population.
// array1 = paired males
// array2 = paired females
// array3 = umpaired males
// array4 = unpaired females
// count1 = num pairs
// count2 = num unpaired males
// count3 = num unpaired females
{
int removal2 (int* array1a, int*  count1a);
int q;
double c1 = *(count1);
double c3 = *(count2);
double c4 = *(count3);
double c2 = *(count1);
double count = c1 + c2 + c3 + c4;
double p1 = 0;
double p2 = 0;
double p3 = 0;
double var1 = 0;
int count5 = numbirds;
if (numbirds > count) (count5 = count);
for (q = 0; q < count5; q++)
        {
        count = c1 + c2 + c3 + c4;
```

```
        p1 = (c1)/count;
        p2 = (c2)/count + p1;
        p3 = (c3)/count + p2;
        var1 = (double (random(10001))) / 10000;
        if (var1 <= p1 && c1 > 0) (removal2 (array1, count1), c1--);
        if (var1 <= p2 && var1 > p1 && c2 > 0) (removal2 (array2, count1), c2--);
        if (var1 <= p3 && var1 > p2 && c3 > 0) (removal2 (array3, count2), c3--);
        if (var1 > p3 && c4 > 0) (removal2 (array4, count3), c4--);
        }
return (0);
}

int removal2 (int* array1a, int* count1a)

// routine to remove from selected array.
{
int p = 0;
int var1 = 0;
int var2 = *(count1a);
for (p=0 ;p<1;p++)
        {
        var1 = random(var2);
        if (array1a [var1] != 0) (array1a [var1] = 0, p = 2);
        else (p = -1);
        }
return(0);
}
```

B.5. Routines for simulating varying predation levels, with and without the poison drop.

These are the altered functions for survival used in Chapter 4, to first simulate different levels of predation, and then these levels with the poison drop. Mortad and mortju are the proportions that are used to alter the survival rates for adults and juveniles respectively.

```
int adultmortality (int* array, int* count, double* evad, double mortad)
        {
        //    function to do mortality
        int q = 0;
        int p = *(count);
        int i = 0;
        double reapersprob = 0;
        double var2 = 0;
        double reapersprob2 = 0;
        double mort = exp (admort + *(evad));
        reapersprob = mort / (1+ mort);
        reapersprob2 = pow(reapersprob, 12) * mortad;

        for (q = 0; q < p; q++)
                {
                var2 = (double( random(10001))) / 10000;
                if (var2 > reapersprob2) (*(array + q) = 0, i++);
                if (*(array + q) > 30) (*(array + q) = 0);
                }
```

```
        return(0);
        }

int juvenilemortality (int* juv,int* pair, double* evad, double* evju, double mortju)
        {
        // function to deal to juveniles
        int q = 0;
        double var5 = 0;
        double reapersprob1 = 0;    // linear part of logit
        double reapersprob2 = 0;    // first nine months
        double reapersprob4 = 0;    // :-)
        double mort2 = 0;
        int deathscount = 0;
        double dd = 0;
        int p = *(juv);
        if (p >0) {
        dd = *(pair) * (ddmort + *(evju));
        double mort = exp (admort + *(evad));
        mort2 = exp(juvemort + dd);
        reapersprob1 =  mort2 / (1 + mort2);
        reapersprob2 = pow(reapersprob1,9);
        double reapersprob = pow(mort/ (1+mort),3);
        reapersprob4 = (reapersprob2 * reapersprob) * mortju;

        for (q = 0; q < p; q++)
                {
                var5 = (double( random(10001))) / 10000;
                if (var5 > reapersprob4) (deathscount++);
                }
          }
        *(juv) = p - deathscount;
        return(0);
        }

int poisonadultmortality (int* array, int* count, double* evad, double mortad)
        {
        //    function to do mortality
        int q = 0;
        int p = *(count);
        int i = 0;
        double reapersprob = 0;
        double var2 = 0;
        double reapersprob2 = 0;
        double mort = exp (admort );
        reapersprob = mort / (1+ mort);
        double reapersprob1 =pow(reapersprob,6) * sqrt(mortad);
        double mort2 = exp (admort);
        double mort3 = exp (admort + poisad);
        double reapersprob4 = mort3 / (mort3 + 1);
        double reapersprob3 = pow((mort2/(1+mort2)),2);
        reapersprob2 = (pow(reapersprob, 3) * reapersprob1 * reapersprob3 * reapersprob4) +
                *(evad);
        for (q = 0; q < p; q++)
                {
                var2 = (double( random(10001))) / 10000;
                if (var2 > reapersprob2) (*(array + q) = 0, i++);
                if (*(array + q) > 30) (*(array + q) = 0);
                }
                return(0);
```

```
        }

int poisonjuvenilemortality (int* juv,int* pair, double* evad, double* evju, double mortju)
        {
        // function to deal to juveniles
        int q = 0;
        double var5 = 0;
        double reapersprob1 = 0; // linear part of logit
        double reapersprob2 = 0; // first nine months
        double reapersprob4 = 0; // :-)
        double mort2 = 0;
        int deathscount = 0;
        double dd = 0;
        int p = *(juv);
        if (p >0) {
        dd = *(pair) * (ddmort);
        mort2 = exp(juvemort + dd);
        reapersprob1 =  mort2 / (1 + mort2);
        reapersprob2 = pow(reapersprob1,3);
        double reapersprob =pow(reapersprob1, 6) * sqrt(mortju);
        double mort3 = exp (admort);
        double mort4 = exp (admort + poisad);
        double reapersprob6 = mort4 / (mort4 + 1);
        double reapersprob5 = pow((mort3/(1+mort3)),2);
        double reapersprob7 = reapersprob5 * reapersprob6;
        reapersprob4 = (reapersprob2 * reapersprob * reapersprob7) + *(evju);

        for (q = 0; q < p; q++)
                {
                var5 = (double( random(10001))) / 10000;
                if (var5 > reapersprob4) (deathscount++);
                }
          }
        *(juv) = p - deathscount;
        return(0);
        }
```

And below is the altered fecundity equation, which allows it to be varied to simulate predation. Birth effect is the proportion that the reproductive success of the population is altered by.

```
int reproduction (int* pm, int* pf, double* pq, int* pair, int* juv, double* evbi, double birtheffect)
        {
        double normrand (void);
        // function to calculate number of juveniles produced
        int q = 0;
        int p = 0;
        double fledglings = 0;
        double fledgling = 0;
        double  magek = 0;
        double  fagek = 0;
        double  dd = 0;
        double evb  = 0;
        p = *(pair);
        dd = (ddbirth) * p;
        for (q = 0; q< p; q++)
                {
                if (*(pm+q) == 1) (magek = male1);
```

```
            else (magek = male2);
            if (*(pf+q) == 1) (fagek = female1);
            else (fagek = female2);
            evb = normrand() * 0.71605;
            fledgling =(*(evbi) + magek + fagek + *(pq+q) + dd +  birthint + evb);
            if ((int(fledgling) - fledgling) < -0.5) (fledgling = int(fledgling) +1);
            else (fledgling = int(fledgling));
            if (fledgling < 0 ) (fledgling = 0);
            fledglings = fledglings + fledgling;
            }
      *(juv) = int (fledglings * birtheffect);
      return(0);
}
```

Appendix C

Sensitivity Analysis

This appendix contains the graphs of the effects of varying the parameters in the sensitivity analysis by plus or minus three standard errors from their estimated values. All graphs have been produced from 200 simulations, and the results are taken from the 50th year.

The following figures are included:

C.1. The effect of varying the adult survival intercept parameter.

C.2. The effect of varying the juvenile survival intercept parameter.

C.3. The effect of varying the density dependent parameter in juvenile survival.

C.4. The effect of varying the intercept term from the reproductive equation.

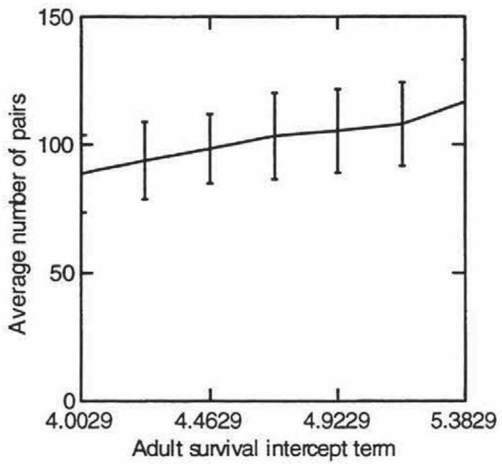
C.5. The effect of varying the density dependent parameter in the reproductive equation.

C.6. The effect of varying the sex ratio.

All figures include the effect on average population size and on the average number of unpaired males. Unpaired females is not shown as this value only ever increased when the sex ratio was increased (with there being a maximum of 5 unpaired females)

Figure C.1. Effect of varying the adult survival intercept parameter. The value is altered by up to plus or minus three standard errors. The effect of this on (A) the average number of pairs and (B) the number of unpaired males. The estimated parameter value is 4.69. The error bars represent one standard deviation from the mean.

(A) Effect on the average number of pairs



(B) Effect on the average number of unpaired males

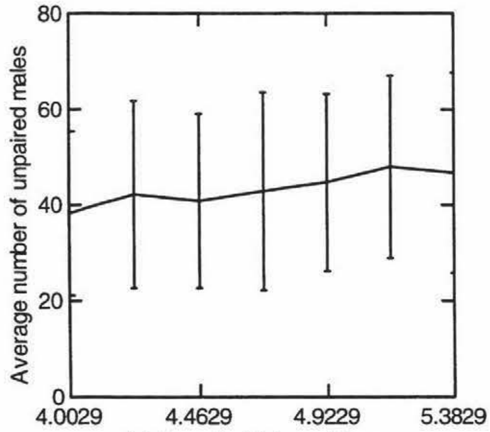
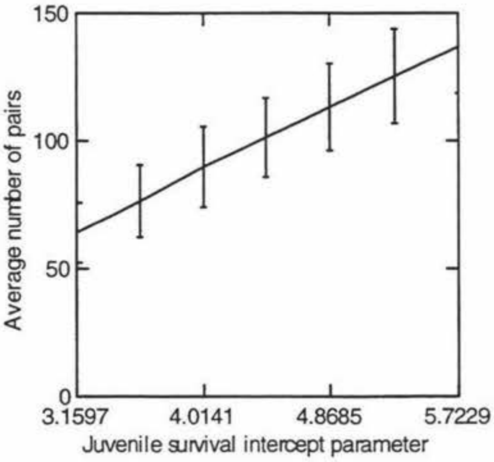


Figure C.2. Effect of varying the juvenile survival intercept parameter. The value is altered by up to plus or minus three standard errors. The effect of this on (A) the average number of pairs and (B) the number of unpaired males. The estimated parameter value is 4.44. The error bars represent one standard deviation from the mean.

(A) Effect on the average number of pairs



(B) Effect on the average number of unpaired males

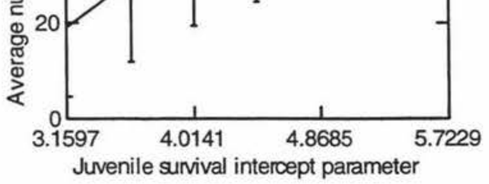
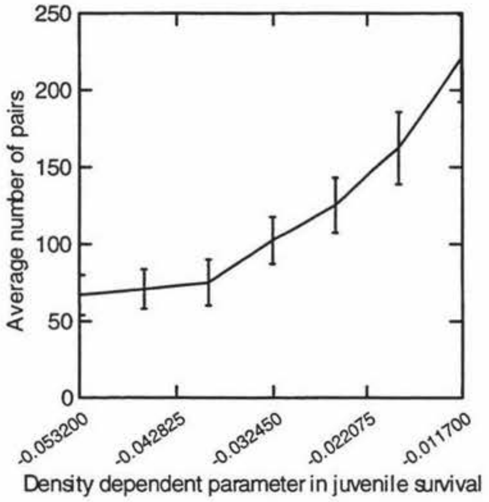


Figure C.3. Effect of varying the density dependent parameter in juvenile survival. The value is altered by up to plus or minus three standard errors. The effect of this on (A) the average number of pairs and (B) the number of unpaired males. The estimated parameter value is -0.033. The error bars represent one standard deviation from the mean.

(A) Effect on the average number of pairs



(B) Effect on the average number of unpaired males

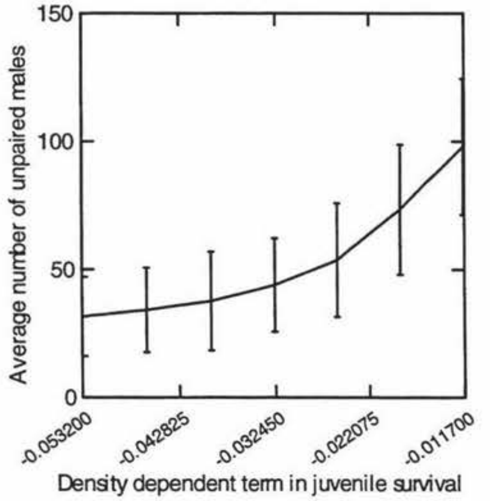
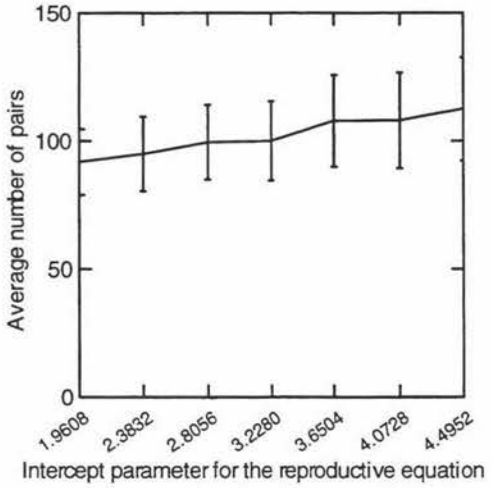


Figure C.4. Effect of varying the intercept term from the reproductive equation. The value is altered by up to plus or minus three standard errors. The effect of this on (B) the average number of pairs and (A) the number of unpaired males. The estimated parameter value is 3.23. The error bars represent one standard deviation from the mean.

(A) Effect on the average number of pairs



(B) Effect on the average number of unpaired males

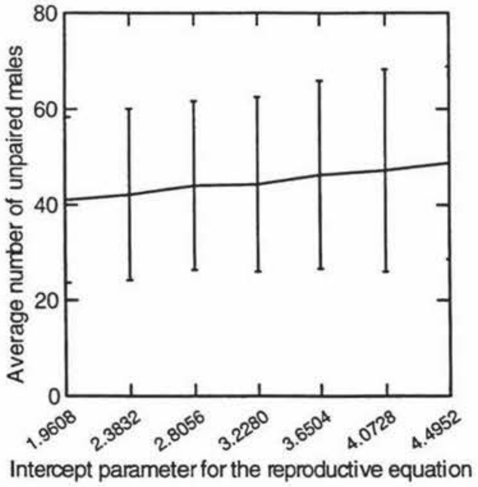
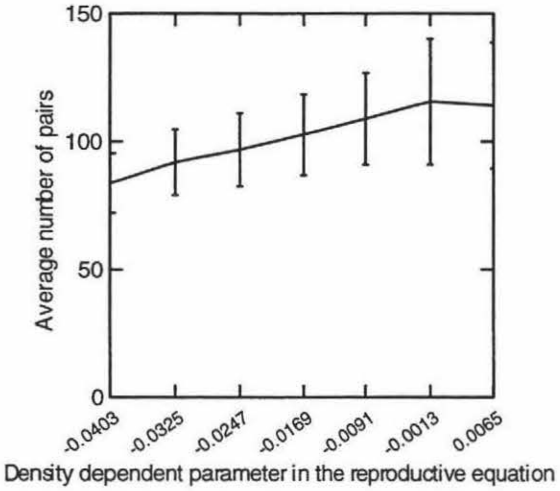


Figure C.5. Effect of varying the density dependent parameter in the reproductive equation. The value is altered by up to plus or minus three standard errors. The effect of this on (A) the average number of pairs and (B) the number of unpaired males. The estimated parameter value is -0.017. The error bars represent one standard deviation from the mean.

(A) Effect on the average number of pairs



(B) Effect on the average number of unpaired males

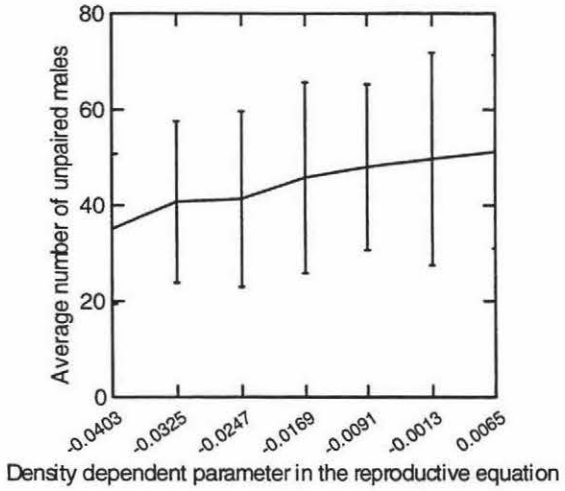
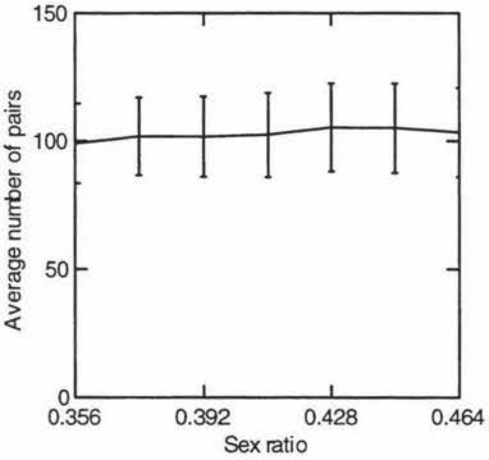


Figure C.6. Effect of varying the sex ratio. The value is altered by up to plus or minus three standard errors. The effect of this on (A) the average number of pairs and (B) the number of unpaired males. The estimated parameter value is 0.41. The error bars represent one standard deviation from the mean.

(A) Effect on the average number of pairs



(B) Effect on the average number of unpaired males