An introduction to using mark-recapture analysis for monitoring threatened species

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ABSTRACT

Accurate and reliable monitoring is necessary for effective management of threatened species in New Zealand. Mark-recapture studies are a powerful tool for conservation managers, and can be used in any situation where animals can be marked (or otherwise identified) and detected later by capture or sighting. In addition to estimating population size and survival rates, mark-recapture methods can be used to evaluate impacts of threats on survival, record population trends, collect information for population viability analyses, set performance targets against which responses to management can be measured, and highlight areas where further research is necessary. This report has three main sections. The first section introduces the basic principles of mark-recapture methodology that conservation managers need to understand to design effective mark-recapture studies. In the second section, specific guidelines for estimating abundance, survival and population growth rates are provided. We show which methods are appropriate for different situations, how field studies should be designed to avoid violating assumptions of mark-recapture methods, and how to get started on analysing the data. In the final section, we review a case study involving long-tailed bats (*Chalinolobus tuberculatus*), and use this to illustrate some problems that may be encountered in mark-recapture studies.

Keywords: abundance, *Chalinolobus*, closed-population models, long-tailed bat, mark-recapture, open-population models, population monitoring, robust design, survival.

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1. Introduction

1.1 USES OF MARK-RECAPTURE METHODS

Conservation managers are routinely asked to provide information about the status of threatened **populations**[1] or species. The most commonly asked questions include: 'how many animals are there in this population?', and 'is the population decreasing, stable, or increasing?' The answers to these questions will govern the management regime chosen for the population or species in question.

The mark-recapture method is a powerful method for estimating **abundance** as long as the underlying assumptions are met (Thompson et al. 1998). Mark-recapture analysis can also be used to estimate other population **parameters** such as survival, **recruitment**, and population growth rate. A well-designed study will allow the user to assess the importance of various factors that might affect these parameters, including characteristics of individuals such as age or sex, changes over time such as seasonal effects, and impacts of management actions such as predator control. Once this understanding is achieved, parameter **estimates** can be combined into a population **model** that can be used to assess the viability of the population over time, evaluate the relative impacts of different threats, and predict how the population will respond to different management strategies.

This report introduces the general design and analysis procedures that constitute a mark-recapture analysis, and demonstrates its application using a case study of long-tailed bats (*Chalinolobus tuberculatus*) in South Canterbury. The recent development of easy-to-use software allows mark-recapture studies to be performed on a greater range of species than formerly possible. The aim of this report, therefore, is to encourage the use of mark-recapture methods among conservation managers and within threatened species programs.

1.2 EXAMPLES OF MARK-RECAPTURE STUDIES IN NEW ZEALAND

Mark-recapture and/or mark-resight studies have become more prevalent in New Zealand with the development of easy-to-use software, particularly program MARK[2] (Box 1). The studies described here were conducted to evaluate the impacts of pest control operations, assess the fate of island reintroductions, investigate dispersal patterns, estimate abundance in comparison with other techniques, re-analyse historical data, and obtain population parameters for a little-known species.

Mark-recapture analysis was used by Armstrong & Ewen (2001), Armstrong et al. (2002) and Davidson & Armstrong (2002) to estimate the impacts of aerial poison operations on the survival of non-target species (New Zealand robins

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1 Many of the terms used in this report are defined in the glossary of terms, Appendix 1, p. 30.

2 Computer program names in this report are in given in capitals, commands in small caps.

Box 1. Program MARK

Program MARK is the state-of-the art software for analysing mark-recapture data, and largely supersedes a range of previously used programs. MARK was developed by Gary White at Colorado State University, but incorporates software and theory developed by many people. As advances are made in mark-recapture methods, they are added to MARK. You can see short descriptions and links to 14 different programs at Evan Cooch's website: http://www.phidot.org/software/
The other programs still have some uses, especially to people familiar with them; however, most people will have no need to use anything other than MARK, and it is definitely the best place to start.

MARK provides a unified approach for analysing several different types of mark-recapture data, and allows models to be created and run using a WINDOWS interface. MARK is much easier to use than previous programs, making mark-recapture analysis accessible to a wide range of people. MARK can be downloaded free-of-charge from the MARK website:
http://www.cnr.colostate.edu/~gwhite/mark/mark.htm

The program should run on any IBM-compatible computer with WINDOWS 95 or higher, a Pentium processor, and at least 64 mB RAM. However, if you have a faster computer with more memory, MARK will run better and be less likely to crash.

There is extensive support available for learning MARK. The standard reference is White & Burnham (1999), and a draft version of this publication is available on the MARK website. Evan Cooch and Gary White have written a guidebook called 'Using MARK—a gentle introduction', and this can also be downloaded from the MARK website. Pryde (2003: this volume) provides a working example for a threatened New Zealand species, the long-tailed bat (*Chalinolobus tuberculatus*). There is an interactive website devoted to questions and answers about MARK:
http://canuck.dnr.cornell.edu/HyperNews/get/marked/marked.html

Finally, MARK workshops are held periodically all over the world.

While we have stressed how easy and accessible MARK is compared with previous mark-recapture software, it is by no means trivial to use. It is a complex program, can be frustrating to use, and has a deceptively long learning curve. **If you are planning to use MARK, seek expert help to avoid making mistakes.**

Petroica australis, stitchbirds *Notiomystis cincta*, and saddlebacks *Philesturnus carunculatus*). Birds were individually marked by fitting colour bands while in the nest, and subsequent 'recaptures' done by sighting the birds in a series of surveys rather than capturing them. By combining mark-recapture analysis with **simulation modelling**, the authors were able to estimate the amount of mortality attributable to the poison drops and predict the long-term impact of this mortality on population growth. For instance, Davidson & Armstrong (2002) estimated that about 45% of the saddlebacks died following a poison drop on Mokoia Island, setting population growth back by one to two years but having no long-term impact on the population. The authors note that this methodology is much more effective for estimating mortality than other techniques such as body counts or 5-minute bird counts, and for many species is more effective than radio-tracking.

The viability of four populations of New Zealand forest birds re-introduced to predator-free islands was examined by Armstrong et al. (2002) in order to decide what, if any, management was needed to maintain them. Details of the approach used were given by Armstrong & Ewen (2001) and Armstrong & Perrott (2000). In all cases birds were individually marked by colour banding in the nest, and 'recaptured' by sighting them in surveys. Mark-recapture analysis was used to estimate abundance and model factors affecting mortality rates. This information was then incorporated into simulation models used to estimate population viability. While the Tiritiri Matangi Island robin and Mokoia Island saddleback populations appeared to be viable without management, the stitchbird populations required on-going management to persist. Stitchbirds on Tiritiri Matangi appeared to be viable so long as management continued (supplementary food and nest mite control). In contrast, the Mokoia population was predicted to have tenuous viability even with management, leading to a decision to remove the birds after 8 years and translocate them to another island.

Efford (1998) conducted an age-structured mark-recapture analysis to investigate patterns of dispersal of brushtail possums (*Trichosurus vulpecula*) in the Orongorongo Valley, near Wellington. The majority of immigrants were males, with three in four breeding males and one in five breeding females leaving their natal areas. The motivations driving immigration remain to be determined, but did not appear to be related to weather conditions, food shortages, or high possum densities.

Linklater et al. (2001) used mark-recapture analysis to estimate the size and growth rate of a feral horse population in the Kaimanawa Ranges, and to evaluate the accuracy of helicopter counts. Aerial counts have taken place on a regular basis since the mid-1980s and are an integral part of a management programme designed to minimise the impacts of feral horses on native plant communities. Parts of the area surveyed by helicopter were subsequently re-surveyed using mark-resight methods (where individuals were identified from either natural markings/colouration or freeze brands), and also by **distance sampling** using line transect counts, and dung-density sampling. These three techniques all gave similar estimates, but the helicopter count over-estimated the number of marked animals by 15–32%, probably because of double counting or horses fleeing from the helicopter. Linklater et al. (2001) noted that the mark-recapture methodology was the most useful because it allowed them to estimate recruitment, survival, and population growth, as well as population size.

Scofield et al. (2001) used mark-recapture analysis to re-analyse titi (sooty shearwater, *Puffinus griseus*) banding data collected between 1940 and 1957. At the time of the original analysis, mark-recapture programs were not available and other methods were used. While survival rates from the original analysis were comparable to those obtained using mark-recapture, the latter approach revealed that non-breeding birds had lower survival and capture rates than breeding individuals. The original researcher had made this observation but could not demonstrate it statistically using the methods available at the time.

Flannagan (2000) estimated abundance and **density** of a little-known species, the goldstripe gecko (*Hoplodactylus chrysosireticus*), on Mana Island in Cook Strait. Prior to the discovery of this population in 1972, goldstripe geckos had only been recorded from the Taranaki region in the North Island. Mana Island goldstripe geckos, despite living in apparently ideal habitat, exhibit slow population growth and may not be stable over the long term. As this is the only population secure from mammalian predators and habitat destruction, the study raised concern over the current low conservation priority ranking of the species.

The purpose of these examples is to illustrate the range of application rather than provide an exhaustive review. Mark-recapture methods have also been used in New Zealand to study weta, tuatara, frogs, and marine mammals, and we discuss a case study involving bats at the end of the paper. Collectively, such studies show that it is now possible to use mark-recapture methods to study small populations (as few as 20–30 animals) and / or species that are difficult to study. However, mark-recapture methods are not always possible or appropriate, and the intending user needs to understand the principles and requirements of a mark-recapture analysis before setting up their own study.

1.3 BASIC PRINCIPLES OF MARK-RECAPTURE ANALYSIS

Mark-recapture analysis can potentially be used whenever animals can be marked or otherwise identified. Marks are usually individual-specific, and can consist of metal bands (birds or bats), colour bands (birds), ear tags (mammals), toe clip combinations (frogs, lizards, small mammals), or pen markings (lizards, tuatara, invertebrates). Radio tags can also be used. It may be possible to identify individuals without marking them at all, for example by the individual markings on fins of cetaceans. As noted in some of the examples above, data can often be collected by re-sighting rather than actual capture, which has the advantage of causing less disturbance. Due to recent advances in DNA technology, it is now possible to individually identify animals from faeces, meaning that mark-recapture analyses can even be used on animals that are neither seen nor captured. This technique has been developed for possums and stoats in New Zealand, and may become available for other species in the future (D. Gleeson, Landcare Research, Auckland, pers. comm.).

This diversity of techniques can lead to confusing terminology. Throughout this report, these different techniques (mark-recapture, mark-resight, and identification from photos or faeces) are collectively referred to as 'mark-recapture', as sightings can, in fact, be thought of as 'visual captures'. Consequently, capture sessions and re-sighting surveys are both referred to as 'capture sessions'. The methods for analysing data collected by these different methods are identical.

The design of a mark-recapture study is very important, and will determine what the results can be used for. An important distinction can be made between open and closed population mark-recapture studies. A **closed population** remains constant in size and composition during the study, while an **open population** is subject to animals leaving and entering the population through births, deaths, emigration and immigration. Although all populations are subject to these processes, it is possible to have closure by conducting a study over a short time frame, and this is often desirable. Section 1.3.1 explains closed population mark-recapture studies, and Section 1.3.2 explains open population mark-recapture studies.

1.3.1 Closed populations

Closed population mark-recapture studies are used to estimate the number of animals in a population; i.e. to provide an estimate of **absolute abundance**. The simplest case involves two capture sessions. In the first capture session, a group of animals is caught, marked and released. The population is then re-sampled on one subsequent occasion. This method was developed independently by Peterson in the 1890s to estimate the size of fish populations and by Lincoln in the 1920s to estimate wildlife populations. It is therefore called the Peterson-Lincoln estimate (Seber 1982).

Consider a mark-recapture study on saddlebacks conducted in September on an off-shore island. In the first capture session, 100 saddlebacks were caught by setting mist nets all over the island, marked with colour bands, and released. A second capture session took place one week later. Sixty saddlebacks were caught, of which 40 were recaptures from the first session. These results can be used to estimate abundance if certain assumptions can be made about the population (Box 2).

Box 2. Assumptions of the Peterson-Lincoln estimate

1. There is no birth, death or emigration during the study
2. All animals have the same probability of being caught
3. Marks are not lost

The first of these assumptions is often referred to as the 'assumption of closure' in the literature and can be relaxed in some cases (Pollock et al. 1990). The second assumption, often called the 'assumption of equal catchability', is unlikely to be true for many wild animal populations. This has led to the development of more appropriate population models that specifically address this issue, and these will be covered below. The third assumption applies to any mark-recapture model.

In the saddleback study, trapping sessions were separated by a one-week period. It is reasonable to assume that no saddlebacks would have died over this short time period. Secondly, there would be no reproduction since saddlebacks start breeding later. Thirdly, no saddlebacks would be arriving to or leaving the island. If it can be assumed that the capture probabilities are the same for all birds (including marked versus unmarked individuals), the probability of a saddleback being caught during the second capture session can be estimated as 40%. That is, 40 banded birds were caught from 100 available. To estimate the size of the population, the following equation[3] is used:

$$\hat{N} = \frac{n_1 n_2}{m_2} = \frac{100 \times 60}{40} = 150$$

where $\hat{N}$ = estimated population size

n_1 = number of animals caught in the first capture session
n_2 = number of animals caught in the second capture session
m_2 = number of animals caught in both sessions (recaptures)

[3] Notation is defined in the glossary of notation, Appendix 2.

Note that the 'hat' on the N is used to indicate an estimate of a parameter. Further examples, including methods for estimating variance and **confidence intervals**, are given by Pollock et al. (1990).

Closed population mark-recapture studies can have multiple capture sessions, and this has advantages over conducting just two sessions. As well as providing more data, allowing more precise estimates, it also allows us to address the second assumption above, that all animals have the same probability of being caught (Box 3). The behaviour of animals may change after initial capture, causing them to be captured more frequently ('trap happy') or less frequently ('trap shy'). Individuals may also be inherently different in their probability of capture. If ignored, these effects could cause abundance to be **biased**, i.e. overestimated or underestimated (Table 1).

Box 3. Assumptions of closed population mark-recapture models with multiple (> 2) capture sessions

1. There is no birth, death, immigration or emigration during the study
2. Marks are not lost

Otis et al. (1978) showed how these effects can be detected using mark-recapture data, and developed theory for estimating abundance with these effects operating. They also showed how changes in **capture probability** between sessions, which can also bias estimates (Table 1), can be accounted for. They developed Program CAPTURE, which allows the user to compare alternative models (Box 4) to assess which effects are operating, then estimate population size using the most appropriate model. Program MARK (White & Burnham 1999) allows a similar **model selection** procedure. The difference is that MARK allows users to consider difference in capture probabilities resulting from biologically meaningful characteristics of animals (e.g. age and sex) rather than just random variation. The mathematics of these methods are beyond the scope of this guide, but interested readers can consult Otis et al. (1978), Schwarz & Seber (1999) and Borchers et al. (2002).

TABLE 1. REASONS WHY ANIMALS MAY HAVE UNEQUAL CAPTURE PROBABILITIES, AND CONSEQUENCES OF IGNORING THESE FACTORS WHEN ESTIMATING ABUNDANCE (N).

SOURCE OF BIAS	EXAMPLE	CONSEQUENCE	N
Capture heterogeneity	Some animals less likely to be caught (e.g. age-biased dispersal)	Marked animals have higher capture probabilities	Under-estimated
Capture heterogeneity	Inappropriate trapping method (e.g. not enough traps used)	Precludes some individuals from capture if trap already occupied	Under-estimated
Capture heterogeneity	Inappropriate trap placement (e.g. traps on edge of home range instead of middle)	Animals less likely to be captured, hence fewer animals marked	Under-estimated
Trap response	Trap-happiness (e.g. use of baited traps)	Animals caught once are more likely to be caught again	Under-estimated
	Trap-shyness (e.g. animals learn to avoid nets or traps in fixed places)	Animals caught once are less likely to be caught again	Over-estimated

Box 4. Model selection

Any statistical analysis involves model selection. The aim is to find a **parsimonious** model—i.e. a model that includes factors useful for explaining the data but excludes irrelevant factors (Burnham & Anderson 2002).

The traditional way of doing this is the **hypothesis testing approach**, where you compare a **null hypothesis** with an **alternative hypothesis** that includes another factor. If the variance associated with that factor can be due to chance alone, the null hypothesis is accepted. However, if this is unlikely (the *P* value is typically set at 0.05), the factor is deemed statistically significant and the alternative hypothesis accepted. If multiple factors are considered, there is a separate hypothesis test for each term that could be included. For example, a three-way Analysis of Variance involves 7 hypothesis tests (one for each main effect or interaction) and could result in any of 15 different models being selected.

An alternative is the **information-theoretic approach**, which came from a merging of information theory and likelihood theory (Burnham & Anderson 2002). Under this approach, the most parsimonious model is that with the optimal compromise between precision and bias. This is usually based on Akaike's Information Criterion (AIC), which is calculated from the model's likelihood (the probability of getting the observed data if the model is correct) and the number of parameters in the model. The plausibility of alternative models can also be weighed based on their AIC values. This means that parameters can be estimated either from the best model alone, or by a model averaging process taking the AIC values of the models into account.

Both approaches are applicable to mark-recapture analysis, and can be done easily in MARK. There is debate on their relative merits, and Cooch & White (2001) recommend that analysts become familiar with approaches. However, Burnham & Anderson (2002) make a strong case for the information-theoretic approach. They argue that we should think carefully about the relevant factors **before** data analysis, and produce a set of 4–20 candidate models. The potential advantages of their approach are: (1) it reduces the number of candidate models, giving less chance of selecting an over-fitted model (a complex model that happens to fit the current data set but has poor predictive capacity), (2) it uses a theoretically sensible selection criterion, avoiding arbitrary *P* values, (3) it allows alternative models to be weighed, and (4) it encourages us to think carefully about the biology and management issues rather than being statistical automatons.

1.3.2 Open populations

If populations are subject to births, death, immigration and emigration during a study, then open population mark-recapture methods must be used. Analysing data from mark-recapture studies of open populations is more complicated theoretically, because births, deaths, immigration or emigration may be confounded by our ability to detect these processes. For instance, if we fail to detect an animal at the start of the study, we may mistakenly assume that it arrived later by birth or immigration, and if we fail to detect an animal previously detected, we may mistakenly assume that it died or emigrated.

The key to open population theory is estimating survival probability (ϕ) and capture probability (p). Once capture probability is known, population sizes for each capture occasion (denoted as $_i$) can be estimated by the equation:

$$\hat{N}_i = n_i / \hat{p}_i$$

where

$\hat{N}_i$ = population size for capture occasion i

n_i = number of animals captured on occasion i

$\hat{p}_i$ = capture probability on occasion i

Recruitment between capture sessions is estimated according to the equation:

$$\hat{B}_i = \hat{N}_i - \phi_i \hat{N}_{i-1}$$

where

$\hat{B}_i$ = recruitment for occasion i

$\hat{N}_i$ = population size for capture occasion i

ϕ_i = survival probability on occasion i

Note that animals in any session can be divided into three categories: (1) live animals that are seen, (2) live animals that are not seen, and (3) dead animals (Fig. 1). The trick is estimating the relative proportions in categories 2 and 3. The mathematics for doing this are again beyond the scope of this guide, but the underlying concepts are not too difficult to understand. If individuals tended to be captured in most sessions, then disappear, we would naturally think that capture probability was high and that most disappearances were due to mortality (or emigration). Conversely, if individuals tended to be captured intermittently, we would think that capture probability was lower and that many of the individuals missing at any time were alive. The Jolly-Seber model (JS) does this formally (Seber 1982). A variant of this model, the Cormack-Jolly-Seber (CJS) is also commonly used.

Open population mark-recapture models require four assumptions to be met (Box 5). The original JS and CJS models required all animals to have the same survival and capture probabilities, but subsequent developments have allowed this to be relaxed to 'animals of the same type have the same survival and capture probability'. It is now possible to divide animals into different groups; for example, to allow different survival and capture probabilities for males and females. It is also possible to fit individual **covariates**; for example, to allow survival or capture probability to depend on body weight. It is also possible to

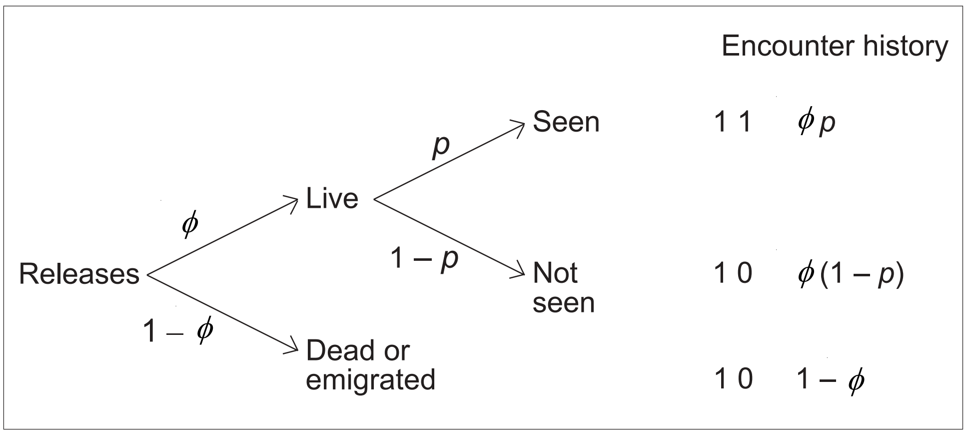


Figure 1. Representation of open population mark-recapture model. Each released animal has probability ϕ of surviving to the next capture session or survey, and each surviving animal has probability p of being detected. The encounter histories of dead and undetected animals are indistinguishable at this stage, but it becomes possible to estimate ϕ and p with further sessions. From White & Burnham (1999).

Box 5. Assumptions of open population mark-recapture models

1. All animals (of the same type) have the same survival probability
2. All animals (of the same type) have the same capture probability
3. Marks are not lost or overlooked
4. The duration of each capture occasion is instantaneous in relation to the intervals between sessions

add age structure to the CJS, so that juveniles and adults can have different survival or capture probabilities. Those interested in the mathematical theory underlying open population mark-recapture models should consult Pollock et al. (1990).

2. Guidelines for mark-recapture studies

The most important reason for understanding the basic principles of mark-recapture is to ensure that monitoring is done efficiently. It is important to ensure that a mark-recapture study is the most sensible approach for addressing the issue, that the design does not violate basic assumptions, and that the data collection is sufficient but not excessive. Other considerations include potential impacts of capture and marking methods, the size and location of the study area, and factors that influence capture rates. For instance, capture rates obtained in lizard pitfall trapping studies are strongly affected by temperature. In such cases, relevant variables and covariates should be measured and, where possible, attempts made to minimise their influence.

As with any type of research, the first step is to define the aim of the study (e.g. is abundance or survival estimation of primary interest?). Sections 2.1 and 2.2 provide guidelines for using mark-recapture to estimate abundance and survival, respectively. We will briefly discuss a method that maximises **power** for estimating abundance and survival simultaneously (Section 2.3), and then consider a method for estimating population growth rate (Section 2.4).

2.1 ESTIMATING ABUNDANCE

Mark-recapture methods are impractical in some situations. They are also usually more costly than other methods of estimating abundance, so it is important to ensure they are appropriate. We will therefore consider alternative methods of estimating abundance (Fig. 2) before discussing guidelines for mark-recapture studies.

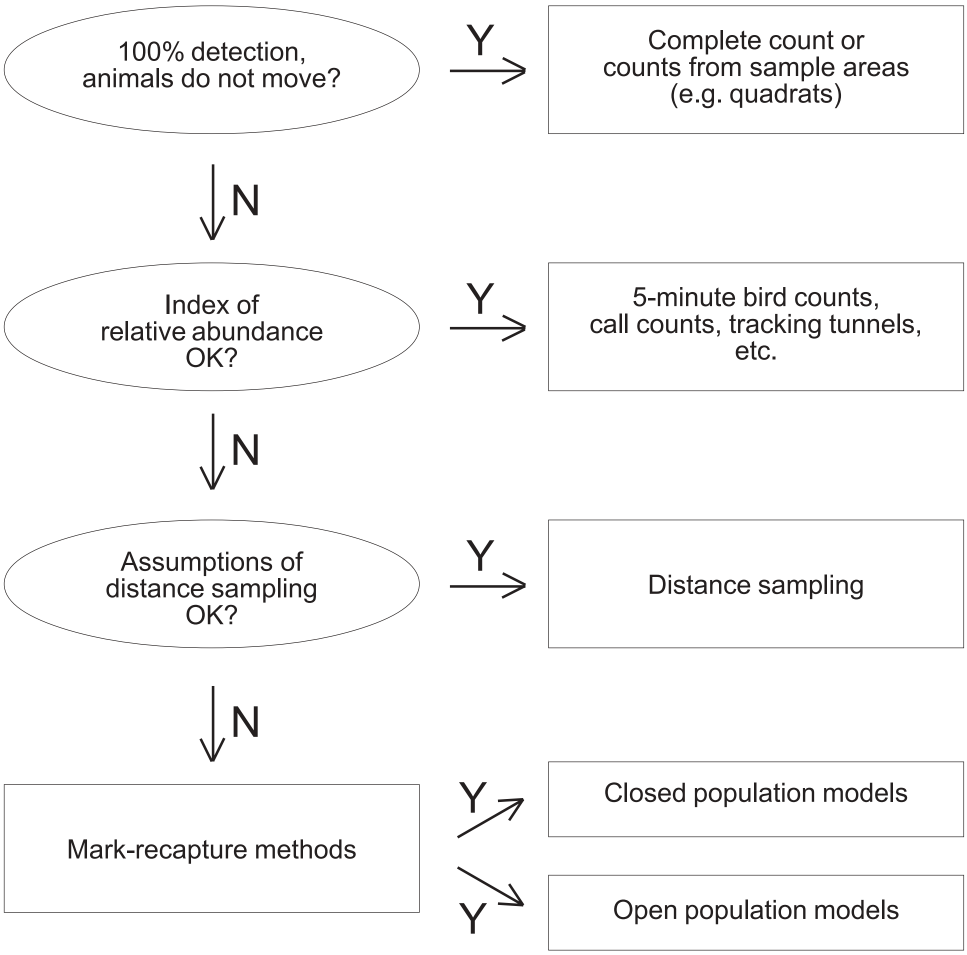


Figure 2. A simple scheme for determining a suitable method for assessing abundance. If mark-recapture is used, a closed population model should be used when the aim is to obtain a single estimate of abundance, whereas an open population model is needed if the population is studied over time. The two approaches can be combined using the robust design (Section 2.3). Data from closed, open, and robust designs can all be analysed using Program MARK (Box 1).

2.2.2. Methods for assessing abundance

Mark-recapture requires animals to be marked, so it is unlikely to be used, say, for estimating abundance of springtails in soil samples. However, people are generally prepared to fix springtails in alcohol, making them immobile, and it is possible to simply count all the springtails in small samples. Standard statistical techniques can then be used to analyse those counts. Mark-recapture methods are unnecessary in any situation where it is possible to count all the individuals in a sample area. This will be the case whenever detection probability is 100% and animals are immobile with respect to the observer. Most plants fall into this category, as well as sessile marine animals, and some large animals that can be surveyed by aircraft. If the whole population cannot be counted, then counts are made in sample areas such as quadrats.

If such techniques cannot be used, then distance sampling may be the best approach. Distance sampling gives an absolute estimate of abundance, and can be used for animals that are mobile and / or do not have 100% detection. It does not require marking, so is cheaper and easier than mark-recapture. Distance sampling involves recording distances of animals from transects or points, and using the distance data to estimate detection probability. The basic theory is relatively simple and the program DISTANCE is easy to use. The program and extensive documentation can be downloaded at:
http://www.ruwpa.st-and.ac.uk/distance/

Unfortunately, program DISTANCE produces highly inaccurate estimates if the underlying assumptions are violated (Box 6). The third assumption is particularly problematic for New Zealand birds because many species tend to move toward or away from observers. Cassey (1999) and Barraclough (2000) have already discussed the applications of distance sampling techniques in New Zealand.

Box 6. Assumptions of distance sampling

1. Points and transects are placed randomly with repect to the distribution of animals
2. Detection probability is 100% at the point or on the transect line
3. Animals do not move toward or away from observers before detection

If neither direct counts nor distance sampling can be used, methods that provide an **index** of **relative abundance** should be considered. An index of relative abundance measures changes in animal populations over time without actually estimating how many animals there are, i.e. abundance is relative to that obtained during previous sampling periods. Indices of relative abundance commonly used in New Zealand include 5-minute bird counts, call counts, and tracking tunnel lines for rodents and mustelids.

Data for such indices can be obtained quickly in comparison with other methods. However, indices can also be problematic. While it is often assumed that the index is directly proportional to population density, this may not be the case (Thompson et al. 1998). In some cases, an index may show changes in conspicuousness that are completely unrelated to abundance. This problem can potentially be addressed by calibrating indices against absolute estimates of abundance (e.g. mark-recapture estimates), but not without considerable additional costs and effort.

A second problem with indices is that they typically have high sampling **variance**, which means that large sample sizes and / or frequent sampling sessions are necessary to detect **population trends**. The use of indices may also require more powerful analysis methods than those used traditionally in order to separate unwanted sources of variation (e.g. weather and observer effects) from real variation in the data.

If none of these alternative methods are suitable, then mark-recapture should be considered. To summarise, mark-recapture may be the best method of assessing abundance if: (1) simple counts are impossible, (2) the assumptions of distance sampling are violated, or (3) an index of relative abundance is insufficient. Mark-recapture may also be the best method simply because capturing animals is the best way to detect them, as is the case for many cryptic or nocturnal species.

2.1.3 Mark-recapture abundance estimation

In theory, the simplest way to measure abundance with mark-recapture is to do one thorough search where all individuals are detected. This is called a **census**. The best known census involves a door-to-door survey of people, who are individually identified by their names, dates and places of birth. Some surveys of animals may also involve fully-marked populations with detection probabilities close to 100%. This has been demonstrated, for example, in the pre-breeding surveys of stitchbirds on Mokoia and Tiritiri Matangi Islands (Armstrong et al. 2002). In most cases, however, it is unreasonable to assume 100% detection and the term census should not be used.

Another simple mark-recapture method is to calculate the **minimum number alive** (MNA) at the time of a survey—i.e. the number of individuals detected during that survey plus any detected in subsequent surveys. The relationship of the MNA to the actual population size is unclear, so it is difficult to interpret in most circumstances. For example, the fact that MNA is higher at Site A than Site B does not necessary mean the population is larger at Site A. The only reason people have used MNA in the past is because it is easy. Recent developments in software (Box 1) and computing have made mark-recapture analysis much more accessible, meaning there is no reason to use MNA in most instances.

If the reason for using mark-recapture is to obtain a single estimate of abundance, then a closed population model should be used. If multiple estimates of abundance and survival over time are wanted, the ideal method is the robust model (Section 2.3), which combines features from open and closed population models. Alternatively, it may be reasonable to use open models (Section 1.3.2) as long as capture probabilities are fairly high (Thompson et al. 1998), and the assumptions of the models are met. Most important are the assumptions that all animals of the same type have equal survival and capture probabilities. Generally speaking, the robust model produces more precise abundance estimates than an open model, but requires more sampling periods.

2.1.4 Designing closed population studies

The key issues to consider when designing a closed population mark-recapture study are the number of capture sessions, their timing, and the number and arrangement of traps or other capturing devices. Otis et al. (1978) recommend that a minimum of 5 sampling sessions be used, and that average capture probabilities of at least 0.1 per session (i.e. on average, every animal has a 10% chance of being captured each session) are necessary for reasonable results. Thompson et al. (1998) suggest a study area should contain at least 100 animals with capture probabilities of at least 0.3 but preferably above 0.5. If a population size exceeds 100 individuals, lower capture probabilities will suffice. Alternatively, more sampling periods could be used. Studies with smaller populations (< 100) will need more sampling periods and / or high capture probabilities.

The timing of the capture sessions is critical to meet the assumption of closure. Most importantly, the intervals between surveys should be short enough that birth, death, immigration and emigration are unlikely. However, some times of year will also be better than others. The start of the breeding season is often a good time, for several reasons. First, abundance estimates are most meaningful at this time because they give the size of the breeding population. Second, you avoid having newly-produced young and nesting adults present, both of which are obvious sources of heterogeneity. Third, no births are occurring yet, and death rates are expected to be low in many species due to good conditions. Fourth, animals of many species are quite settled at this time, resulting in less potential for immigration and emigration.

The number and arrangement of the traps depends on the species and the location. The traps need to be distributed in such a way that it is reasonable to assume that individuals do not differ in probability of capture due to the placement of the traps. For example, with territorial species the traps must be close enough together to ensure there is at least one trap in each territory. There then need to be enough traps in the sampling area to ensure that a reasonable number of animals are captured (see above). Fewer traps may be needed if animals are highly mobile and less site-attached. However, this mobility usually introduces another problem. In the ideal case, the traps will completely cover a geographically closed area. In most cases, however, the trapping area will be a sample of a larger area. This means that animals will inevitably be moving in and out of the area, especially near the edges. This makes it difficult to say what area is actually being trapped, and makes the estimated abundance for that area difficult to interpret. One solution is to use trapping webs (see Buckland et al. 1993), which allow estimation of population density, taking into account the movements of animals on and off the web. However, trapping webs are not widely used. The most common arrangement of traps is a grid, which is more practical because it is easier to place out and locate the traps. Consequently, Murray Efford has recently developed a simulation-based method that allows population density to be estimated from grids, taking movement on and off the grid into account. The method is unpublished as yet, but the software is available at:
www.landcareresearch.co.nz/services/software/density/index.asp

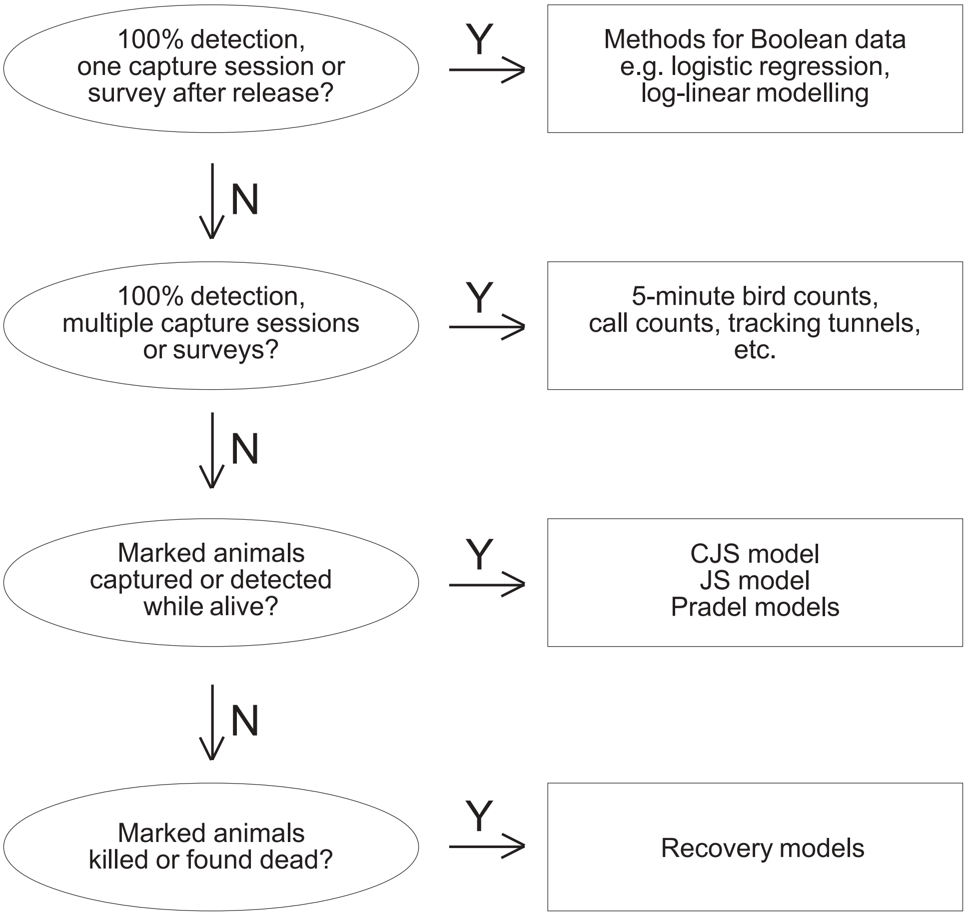
2.1.5 Analysing closed population data

Until recently, the standard program for analysing closed population mark-recapture data was CAPTURE (Otis et al. 1978). However, it is now easier to do similar analyses in program MARK. To do this, start up MARK, select CLOSED CAPTURES where it says SELECT DATA TYPE, and proceed from there. MARK allows the user to divide animals into different groups (e.g. different sexes and ages). By grouping animals, obvious sources of heterogeneity among individuals can be removed. For instance, juveniles may be easier to catch than adults. There may also be seasonal effects whereby animals are easier to catch at certain times of the year than others. And finally, animals may become trap-happy or trap-shy, resulting in different capture and recapture probabilities. All these effects (**capture heterogeneity**, trap-happiness / shyness, and time effects) can be accounted for in closed population models. From there on, alternative simpler models can be constructed and compared by model selection (Box 4; Cooch & White 2001; Pryde 2003).

2.2 ESTIMATING SURVIVAL

Unlike the situation for abundance, there is usually no alternative to mark-recapture for estimating survival. It would be possible to measure survival from counts of unmarked animals if they were immobile, detection was 100% and there was no possibility of recruitment. However, this would be an unusual scenario. The normal methods all involve using captures (or other detection methods) to assess the fate of marked (or otherwise identifiable) animals, so can be classified as mark-recapture methods. The method used depends on the number of capture sessions or surveys, the probability of detection, and whether animals are captured live or found dead (Fig. 3).

Figure 3. A simple scheme for determining a suitable method for estimating survival. All involve capture or survey of marked animals. Boolean (+/-) data can be analysed using standard statistical packages, and the other analyses can all be done using Program MARK (Box 1).



2.2.1 Methods for different types of data

Consider the simplest possible study where a set of animals is marked, surveyed once at a later date, and detection is 100%. In this scenario the fate of each animal is a simple Boolean trial—i.e. it can be in two states: live or dead. The factors affecting survival can then be analysed with standard statistical methods for Boolean data, such as logistic regression or log-linear modelling.

If there are multiple surveys, but detection probability is still 100%, then the data can be analysed using the known FATES OPTION in MARK—i.e. select KNOWN FATES where it says SELECT DATA TYPE. This is similar to the CJS model, but simpler because it is unnecessary to estimate **recapture probability**. The data can also be analysed using the Kaplan-Meier method available in many statistical packages. Radio-tracking is a common method of obtaining known fate data. If detection probability is less than 100%, and animals are captured (or otherwise detected) when alive, then the CJS model is used. To use the CJS model, select LIVE RECAPTURES as the data type in MARK. Most mark-recapture studies of endangered species fall into this category, so the CJS is the most important method to learn for estimating survival. Where animals are recovered dead, as is usually the case for fish and game management, a recoveries model is used. MARK supports two models for analysing recoveries, and several other models for analysing a combination of live and dead recoveries.

As noted above, if you want to combine survival estimates with precise estimates of population size, the best option is the robust model (Section 2.3).

2.2.2 Designing open population studies

These recommendations are written with the CJS model in mind, but they apply to any open population mark-recapture method including the known fate and dead recoveries models. As for closed population mark-recapture, the key issues to consider when designing a study are the number of capture sessions or surveys, their timing, and the trapping or survey strategy.

Lebreton et al. (1992) recommend a minimum of 5 capture sessions. The number required for obtaining precise estimation depends on the number of animals in the data set, the average capture probability, and the number of factors that need to be taken into account. That is, more capture sessions are needed if there are few animals, low capture probabilities, or if complex models are needed.

Sample size is likely to be problematic for studies of threatened species, and will limit the complexity of the models that can be constructed, and therefore what can be learned about detailed processes occurring at the population level. For small populations with low capture probabilities, a mark-recapture study will need a large number of capture sessions. If animals are difficult to recapture in addition to being few in number, a mark-recapture study may not be feasible. It is best to seek statistical advice if this situation applies.

If capture or detection probabilities are high (e.g. detection probabilities greater than 90% are often obtained for robins and stitchbirds), few surveys may be needed. If the object of the exercise is to estimate annual survival probability, there is probably little point in doing more than 1–2 surveys per year in such circumstances. The best investment of effort will be to do good surveys rather than frequent surveys. However, in some cases you may want to model seasonal changes in survival, effects of short-term events, or fine-grained age effects, necessitating several surveys per year (e.g. Armstrong & Perrott 2000).

Surveys should be done at consistent times of year to get meaningful information. For example, your data will be difficult to interpret if you do a survey in September one year, February the following year, and July the year after that. If you are only doing one survey a year, the best time may be the start of the breeding season as noted in Section 2.1.4. If doing multiple surveys per year, it is best if they are evenly spaced. This facilitates modelling of seasonal effects. While variable intervals can be specified in MARK, and these are corrected for in survival estimates, the program performs better when consistent intervals are used. In some cases, survival or detection probability may change over time with factors such as weather rather than following the seasons. It may therefore be useful to record data on such factors, because they can potentially be used as covariates when analysing the mark-recapture data.

The design of the trapping sessions or surveys is critical. In particular, they must be designed to meet the assumptions that capture probability is similar for individuals of a given type, and that capture sessions are effectively instantaneous in comparison with the intervals between sessions. This means that each trapping occasion or survey must cover the entire study area (or at least the habitat suitable for the species), and that search effort should be consistent over this area. It also means that surveys need to take place over a discrete time period—as a rule of thumb, the duration of each survey should be

< 10% of the interval length between surveys (Lebreton et al. 1992). Monitoring programs for New Zealand birds do not usually follow these rules, with one portion of the population searched one time, another portion searched another time, and no discrete surveys. Unfortunately, this means that considerable effort may be expended without producing data that can be used to estimate survival properly.

2.2.3 Analysing open population data

MARK is now the standard program for doing all survival analyses, except for simple Boolean data as discussed above. We have already noted that MARK can handle different data types such as live recaptures, dead recoveries, and known fate data. The default is 'live recaptures', which are analysed using the CJS model.

The first step is to consider what the most complicated model needed to explain the data might be. This will become the global model, and all other models considered will be simplifications of this. Models can be modified by adding groups (e.g. males v. females), individual covariates (e.g. weights), and / or age structure. It may be tempting to produce an extremely complicated model, but such models tend to be confusing and require huge data sets. It is best to keep it as simple as possible.

The next step is to use **goodness-of-fit** testing to assess whether the global model gives a reasonable fit to the data. This is done using a bootstrapping procedure or program RELEASE, both of which are available in MARK. If the data violate the assumptions of open population mark-recapture, then the results will indicate a poor fit. It is possible to correct for mild heterogeneity among individuals (i.e. heterogeneity that is not accounted for by your groups, individual covariates, or age structure). However, a much better approach, if possible, is to find a global model with a good fit to the data.

As for closed population mark-recapture analyses (Section 2.1.5), simpler models are then created and compared using model selection procedures, and survival estimates with 95% confidence intervals obtained from the best model (Box 4; Cooch & White 2001; Pryde 2003).

2.3 COMBINING ABUNDANCE AND SURVIVAL ESTIMATION

The robust design combines the population estimation feature of closed population models with the survival rate estimation feature of open population models. This is made possible by structuring capture sessions into primary and secondary periods. For example, a trapping study might involve trapping animals for 5 consecutive nights every year for 10 years, where the year interval is the primary period and the five consecutive nights the secondary periods. From this study it will be possible to estimate population size for each of the annual 5-night trapping sessions, and survival rates for the nine intervals between the 10 years.

The assumptions of open population models also apply to use of the robust design, but the robust design is more effective at dealing with capture heterogeneity and / or trap response (Pollock 1982). Other advantages of using the robust design are increased precision for population estimation compared with using an open population model alone, and the ability to estimate births or immigration separately. The disadvantage of the robust design is that it requires more capture sessions and may therefore increase the cost, effort and duration of the study. The smallest practical design suggested by Pollock (1982) was 3 primary periods each containing 5 secondary capture sessions.

2.4 ESTIMATING POPULATION GROWTH RATE

In recent years, there has been progressively less emphasis on estimating abundance and progressively more emphasis on estimating population growth rate. The estimated growth rate is usually denoted by the symbol λ (Lambda). A λ value of 1.0 indicates a stable population, while a λ value significantly different from 1 shows that the population is increasing ($\lambda > 1.0$) or decreasing ($\lambda < 1.0$). This has obvious relevance for management of threatened species, and estimating λ can be a simple substitute for **population viability analysis**. Separate estimates of survival and recruitment can be combined to estimate λ. However, λ can be also estimated directly from mark-recapture data.

λ can be estimated directly from the Jolly Seber model or, alternatively, using Pradel's (1996) model which is also available in MARK (select PRADEL SURVIVAL AND LAMBDA as the data type). Unlike the Jolly Seber model, Pradel's model does not estimate abundance and does not estimate separate capture and recapture probabilities. Its assumptions are otherwise similar to those of the Jolly Seber model.

3. A case study using long-tailed bats

3.1 INTRODUCTION

New Zealand long-tailed bats (*Chalinolobus tuberculatus*) are currently classed as nationally threatened. Long-tailed bats have declined since European settlement due to forest clearance, habitat disturbance, and predation by introduced mammals (O'Donnell 2000a). Scattered populations persist throughout New Zealand. Four such populations (Grand Canyon Cave and Ruakuri Reserve, North Island; Hanging Rock and the Eglinton Valley, South Island) are currently being studied with the aim of developing improved monitoring techniques for long-tailed bats nation-wide.

Hanging Rock in South Canterbury has a small population of long-tailed bats. This is the only known bat population from the East Coast of the South Island, and one of few places where bats persist in a highly modified agricultural landscape. It is unlikely that the Hanging Rock population is viable for several reasons: (1) bats do not have access to cavities in large native trees that provide suitable micro-climates for raising young (Sedgeley 2001); (2) roost trees are frequently removed for firewood; (3) cats, possums, rodents and mustelids prey on long-tailed bats; and (4) there is on-going habitat loss and degradation (O'Donnell 2000a).

3.2 OBJECTIVES

The aim of this case study is to illustrate the type of information that can be gained from a mark-recapture study of a threatened species that is difficult to study and requires a large effort to obtain reasonable recapture probabilities. Similar situations occur with many other threatened species (e.g. birds in tall forest on the mainland, forest lizards, some galaxids and invertebrates, other bat species). The case study is not intended as an ideal example of how a mark-recapture study should be done; better examples are listed in Section 1.2. Rather, the bat data provide a good illustration of problems that can arise and the limitations on the level of inference that can be drawn from mark-recapture studies of threatened species. Specifically, we were interested in addressing the following questions:

- How large was the population?
- Was the population stable, increasing or decreasing?
- What proportion of the population survived each year?
- What factors influenced survival (e.g. sex and age of bats)?

3.3 MARK-RECAPTURE ANALYSIS

A simple mark-recapture analysis was performed using four years of trapping data (1998–2002). Bats were trapped by placing harp traps across flyways, or by radio-tracking bats (usually reproductive females or juveniles) to communal roosts and trapping them as they emerged on dusk. Each bat caught was fitted with an individually numbered aluminium forearm band. Trapping was carried out in several in one- to three-week trips between late October and early April each year (the summer season). The data collected from each season were subsequently pooled, giving one capture session for each of the four years. A total of 512 captures of 201 individual bats were made, with some individuals caught up to nine times over the study.

There were several problems with this data set, namely capture heterogeneity, insufficient data and trap-shyness (Table 2). In addition, trapping was done when time and resources permitted, and not at a standard time of year for a discrete time period. Capture heterogeneity was the result of different capture probabilities for the sexes, the different trapping methods used (free-standing harp traps versus trapping at roosts), and sub-structuring of the population into

TABLE 2. SUMMARY OF DATA ISSUES ENCOUNTERED DURING ANALYSIS OF LONG-TAILED BAT DATA FROM HANGING ROCK.

DATA ISSUE	DETAILS	SOLUTION
Capture heterogeneity	Capture probability higher for Collett Road group than Hanging Rock group due to loss of trap sites for Hanging Rock group	Used data from Collett Road group only
Capture heterogeneity	Capture probability varied according to capture method (higher for bats trapped at roosts than free-standing harp traps)	Used data from bats trapped at roosts only
Capture heterogeneity	Females and males had different recapture probabilities	Stratified data into males and females
Insufficient data	Few captures of males	Removed males from data set
	Few captures of juveniles	Pooled adult and juvenile females
Trap response	Bats learned to avoid traps (trap-shyness)	Traps were frequently moved between sites

two distinct social groups with different capture probabilities. The two groups roosted separately but foraged in overlapping areas, similar to sub-structuring found in the Eglinton Valley population (O'Donnell 2000b).

The two groups are referred to as the 'Hanging Rock group' and 'Collett Road group' after their core roosting areas. Most bats were retrospectively assigned to a social group based on the locations of their roost and associations with other bats. Good data were obtained for the Collett Road group, but the Hanging Rock group was not trapped consistently because of a course change in the Opihi River that prevented access to trapping sites. Therefore, the data set used to run the analysis contained only data from female bats known to belong to the Collett Road group (n = 76). The CJS model was run on this data set—i.e. the open population mark-recapture model where survival and capture probability are estimated for each time period. Goodness-of-fit of this model was assessed using RELEASE (See Section 2.2.3). The CJS model was found to have a reasonable fit to this data set, so this was used as the global model for the analysis. Four alternative models were considered, namely:

- Bats have different survival and recapture probabilities each year (global model).
- Survival probability was constant, but recapture probability varied among years.
- Survival probability varied among years, but recapture probability was constant.
- Survival and recapture probability were both constant.

Models were compared using Akaike's Information Criterion (Box 4), and survival and recapture probabilities estimated from the best model. Population size was estimated each year from estimates of recapture probability in the CJS model, according to the method below (Box 7). The Pradel Survival and Lambda option in program MARK was used to calculate the finite rate of population growth for the Collett Road group (see Section 2.4).

Box 7. Estimating population size

Using the CJS model in program MARK generates estimates of survival rates and recapture probabilities. To estimate population size, estimates for recapture probabilities are used in the following formula (Davidson & Armstrong 2002):

$$\hat{N}_i = n_i / p_i$$

where n_i = number of individuals caught on occasion *i*

and p_i = recapture probability for occasion *i*

An approximate 95% confidence interval for each population estimate is given by: $\hat{N} \pm 2\,se$

where $se(\hat{N}) = n(se[p])/p^2$

3.4 RESULTS

3.4.1 Survival and recapture probability

All four models received a reasonable level of support, so model averaging was used to estimate parameters. Estimated annual survival probabilities of female bats in the Collett Road group varied from 0.75 (95% CI 0.54–0.88) to 0.89 (0.48–0.99) during the study (Fig. 4). Estimated recapture probabilities ranged from 0.86 (0.58–0.96) to 0.91 (0.66–0.99), indicating that if an individual bat was alive there was a high probability of capturing it at least once a year.

3.4.2 Size of Collett Road group

Reliable group size estimates could only be calculated for years 2 and 3 and were not significantly different (66 and 60 bats respectively, Table 3). Although an estimate for the first year was calculated (22 bats), this was not reliable, because trappers' unfamiliarity with the study area resulted in fewer captures despite similar sampling effort.

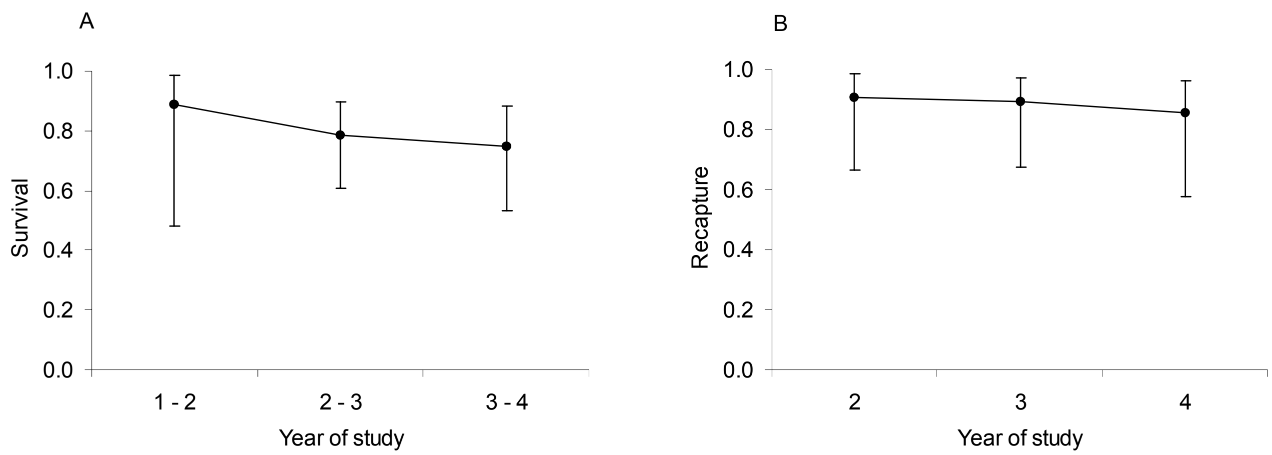


Figure 4. Survival and recapture probabilities for female bats belonging to the Collett Road group (n = 76, error bars represent 95% confidence intervals).

3.4.3 Rate of population decline

The Collett Road group declined in size by approximately 9% over each of the two years for which λ was calculated (0.914 and 0.881 for years 2–3 and years 3–4 respectively, Table 3).

3.5 DISCUSSION

3.5.1 Implications for long-tailed bats at Hanging Rock

- **The Collett Road group is small and declined during the study period**

Analysis of the Collett Road data show that this population consists of a small group of bats (approximately 50–75 females) that appears to have declined by approximately 9% per year over the two years where this could be estimated. There was reason to expect to find a decline, because bats in this area are known to have been killed by cats (and possibly possums). There is also ongoing felling of roost trees. The mark-recapture results confirmed and quantified the decline of the population of long-tailed bats in the Hanging Rock area.

- **More data are needed**

The analysis was limited by small sample sizes and few sampling periods. The relatively small number of females in the Collett Road group was probably not a major problem given the high capture probabilities estimated. However, there were insufficient data for the Hanging Rock group, and for all juveniles and males, limiting the scope of the analysis. The study spanned four years, but it was only possible to estimate abundance and rate of increase for the two middle years of the study. Data for additional years will improve the reliability of the data and the conclusions based on them.

- **Mark-recapture analysis can provide performance targets for management**

The estimates of survival and population decline provide baselines that the bats' response to management can be measured against. Management could include possum control combined with protection of known and potential roost trees. Estimated survival could be incorporated into a population viability model to predict how this population might change over longer time periods and under different management regimes. This would include recruitment rate, which could also be estimated from the mark-recapture data.

TABLE 3. ESTIMATED POPULATION SIZE AND GROWTH (FINITE RATE OF INCREASE, (λ) FOR FEMALE BATS BELONGING TO THE COLLETT ROAD GROUP FOR YEARS 2 (1999–2000 FIELD SEASON) AND 3 (2000–01 FIELD SEASON) OF A FOUR-YEAR STUDY (λ ESTIMATES ARE CALCULATED ACROSS YEARS).

	Year 2	**Year 3**
Group size	66.07	59.58
(95% CI)	(56.16 – 75.98)	(50.81 – 68.35)
	Year 2–3	**Year 3–4**
Finite rate of increase (λ)	0.914	0.881
(95% CI)	(0.396 – 0.994)	(0.425 – 0.987)

4. Recommendations

4.1 DESIGN AND ANALYSIS

A mark-recapture study should:

- Be done with clear questions in mind. These questions will determine whether mark-recapture should be used at all, or whether another method is more appropriate (e.g. whether to estimate or index abundance). This will also affect the type of mark-recapture method used, and the number and timing of capture sessions.
- Be well designed. Capture sessions must be designed to avoid violating the assumptions of mark-recapture analysis. In particular, there must be discrete sessions (i.e. the duration of the session is short in comparison to the intervals between sessions), and the sessions must be designed to equalise capture probabilities among animals as much as possible. Failure to follow these rules will not save any time in the field, and may result in data that require complex analyses, give biased estimation, have low precision, or that cannot be analysed at all.
- Have sufficient capture sessions, taking into account that it may not be possible to use data from all sessions, e.g. for the first sampling session, capture rates may be poor due to researchers' unfamiliarity with the system under investigation.
- Use the appropriate mark-recapture method for the question and data type.
- Be analysed sensibly. The best analysts put a lot of thought into the biological and management issues involved **before** doing their analyses, and construct their models to address those issues. This requires having knowledge of the basic principles of mark-recapture, as well as the biology of the species involved and management options for that species.

4.2 USING MARK-RECAPTURE ANALYSIS FOR MANAGEMENT

Mark-recapture analysis is a powerful tool that can be used for:

- Generating estimates of abundance, survival and recruitment for population viability analysis
- Evaluating the impacts of threats and management actions on survival
- Estimating population trends (i.e. increasing, stable, or decreasing)
- Identifying gaps in data
- Setting performance targets against which response to management can be measured

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Appendix 1

GLOSSARY OF TERMS

Alternative hypothesis Used in traditional hypothesis testing to represent the option that there is some difference or change (see also 'Null hypothesis').

Abundance Number of individuals within a defined area.

relative abundance A measure of change in animal populations over time based on changes in an index.

absolute abundance A measure of change in animal populations over time based on changes in the number of animals present.

Bias A persistent statistical error caused by something other than random chance. Mathematically, bias is the difference between the expected value of a parameter estimate and the true value of the parameter (modified from Thompson et al. 1998).

Capture heterogeneity Differences in capture probability or detection probability among individual animals.

Capture probability The probability that an animal will be captured during a session. It can also be used when animals are not literally 'captured'—i.e. may refer to the probability of detection during a resighting survey. In closed-population models, capture probability refers only unmarked animals and is distinguished from **recapture probability**.

Census A complete count of marked (or otherwise individually identified) animals in a defined area.

Closed population A group of individuals in a particular area studied over a defined time period when there is no birth, death, immigration, and emigration (modified from Thompson et al. 1998).

Confidence interval An interval around a parameter estimate that provides a measure of confidence regarding how close the parameter estimate calculated from the sample is to the true parameter. For example, a 95% confidence interval will contain, on average, the true parameter 95 out of 100 times if 100 such intervals were calculated (modified from Thompson et al. 1998).

Covariate An environmental or biological factor explaining some proportion of variation in data.

Density Number of individuals per unit area.

Distance sampling A method used to estimate population density. Typically, the observer travels along a transect placed across the sampling area and records any animals detected. By recording the distance to each individual sighted, a correction for detectability can be made.

Estimate A numerical value calculated from data to represent the parameter of interest (modified from Thompson et al. 1998).

Goodness of fit A measure of how well a model fits a data set. A poor fit shows that one or more assumptions or the model are invalid, and that it is not an appropriate global model.

Global model A model containing all the factors thought to be important. Other models in a set of candidate models will be simplified cases of this global model. The global model is often the basis for goodness-of-fit evaluation.

Hypothesis testing approach A statistical approach that involves selecting models using null and alternative hypotheses.

Index A relative measure thought to be proportional to a parameter of interest such as abundance or density.

Information-theoretic approach A statistical approach that involves selecting models based on information and likelihood theory instead of hypothesis testing.

Minimum Number Alive (MNA) The number of individuals that are known to have been alive at a defined time.

Model A (usually mathematical) simplification of reality that represents our understanding of how a system operates.

Model selection Using statistical methods to decide what model best explains the data. The aim is to find a model that includes the important factors, and excludes the irrelevant ones.

Null hypothesis Used with the **hypothesis testing approach** to represent the option that there is no difference or change. This hypothesis is tested, and if rejected, an alternative hypothesis is accepted.

Open population A group of individuals studied over a time period when births, deaths, immigration or emigration will have occurred (modified from Thompson et al. 1998).

Parameter An unknown quantity characterising a population—e.g. abundance or annual survival.

Parsimonious A desired characteristic of a model. It is a balance between bias and precision.

Population A group of individuals in a defined area.

Population trend A change in the magnitude and direction of some population parameter (e.g. population size) over time.

Population viability analysis Simulation modelling used to estimate a population's probability of extinction over a defined time frame.

Power The probability of detecting a statistically significant difference in a test of the null hypothesis if such a difference is present.

Recapture probability The probability that a previously marked (or otherwise individually identified) animal will be captured during a session. It can also be used to refer to the probability of detection during a survey, which may be called 'resighting probability'.

Recruitment The number of new animals added to a population in a defined time period due to births and/or immigration.

Simulation modelling A computer model constructed to approximate the dynamics of a real system. Such models can be used to predict population trends under different scenarios.

Variance A measure of precision, where high and low variance indicates high and low precision respectively. Statistically, this is the average of squared differences between a set of values and the mean of the distribution of those values (modified from Thompson et al. 1998).

Appendix 2

GLOSSARY OF NOTATION

B	Recruitment (number of new animals arriving in an area over some time interval, through birth or immigration)
CI	Confidence interval
ϕ	Probability of surviving some time interval
λ	Finite rate of population growth, lambda
m_2	Number of marked animals caught at t_2
n	A general symbol for sample size, but typically used in mark-recapture analysis to indicate the number of animals captured (or detected) in a session
n_1	Number of animals captured during first capture session
n_2	Number of animals captured during second capture session
N	Abundance (number of animals in a defined area)
p	A general symbol for probability, but typically used in mark-recapture analysis to indicate the probability of capturing (or otherwise detecting) a live animal during a session
se	Standard error (the square root of the variance in estimate)
t_1	First capture session or survey
t_2	Second capture session or survey
$\hat{N}$	Estimated population size