Bats: trapping at roosts—estimating survival and productivity

Version 1.0

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Contents

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Synopsis

The survival rates of a species are key parameters for determining the long-term viability of populations. Measuring survival offers a robust alternative to estimating population size when the latter technique is impractical. Mark-recapture techniques can be used to estimate survival of bats. Radio-tracking can be used to monitor survival over the short term, and permanent marks can be used for long-term monitoring. Bats are trapped and marked using harp traps or mist nets using approved best practice procedures that do not disturb the bats unduly (see the 'DOC best practice manual of conservation techniques for bats'—docdm-131465). The fate of individual bats is monitored by recapturing (if permanently marked) or re-sighting (if radio-tagged) a sample of animals at regular, standardised intervals over time. Analyses take into account factors such as birth, death, emigration and immigration, and other factors that might influence survival.

Estimating these measures in bats is dependent on being able to apply recognisable marks that last for the duration of the study. Marks must be applied ethically and humanely. Two types of marks are used:

1. Permanent marks using individually-numbered tags—forearm bands for long-tailed bats and Passive Integrated Transponder tags (PIT tags or microchips) for lesser short-tailed bats. Bands cause injury to lesser short-tailed bats and transponders have now been used successfully.
2. Temporary marks (radio-transmitters for both species).

Many sophisticated analysis methods are available. They fall into two categories:

1. Short-term monitoring using radio-transmitters. Radio-tags are a form of temporary mark in bats because small-sized radio-tags appropriate for use on long-tailed bats and lesser short-tailed bats do not usually remain attached for very long (rarely more than 2 weeks). Thus, it is difficult to obtain sufficient recapture sessions over the time scales required for robust estimates of survival to be calculated. Transmitters have the advantages of allowing individual identification and enabling bats to be monitored remotely without re-handling. Specific survival analysis can be applied to radio-tagged bats (e.g. Kaplan-Meier method or Mayfield method). However, tags are expensive, so sample sizes are generally small, and it is difficult to extrapolate results to the whole population.
2. Long-term monitoring using permanent marks. There are a range of analysis methods appropriate for open populations (those subject to birth, death, immigration and emigration during a study). The Cormack-Jolly-Seber (CJS) model is the most commonly used method of analysis. Analysis of mark-recapture data can be computer-intensive and is aided by the use of specialist software. Program choice may depend on several things, including how well the program is supported in the literature, its user-friendliness, and the costs involved in obtaining the program. Program MARK is arguably the most comprehensive software available for mark-recapture analysis at the time of writing.

Survival analysis is inappropriate for inventory of New Zealand bats, but is valuable for long-term monitoring of permanently marked long-tailed bats and short-term monitoring of both species using radio-tags.

Assumptions

All mark-recapture models have assumptions that must be satisfied if biased estimates are to be avoided. Lettink & Armstrong (2003) summarise all the assumptions for the main methods of estimating survival.

In general, analysis methods assume that marked bats are representative of the population being studied, that marks do not influence behaviour or survival of marked animals, and that loss of contact with a marked animal is random and independent of death. In radio-tracking studies it is assumed that dead bats will be found.

Open-population models provide for potentially rigorous analysis of survival. The Cormack-Jolly-Seber (CJS) model is the most commonly used. It has the following main assumptions:

- Every animal (of the same type) has the same probability of recapture ('equal catchability' or 'capture heterogeneity').
- Every animal (of the same type) has the same probability of survival from one sample to the next.
- Marks are not lost or missed.
- All samples are instantaneous and each release is made immediately after the sample.

Advantages

- Open models are good for estimating survival in bats. If sample sizes are large enough, it is now possible to divide animals into different groups, for example to account for different survival and capture probabilities for males and females or adults and juveniles, and to fit individual covariates that remain constant over an animal's lifetime.
- Permanent, individual marks allow rigorous long-term analysis of survival (and other population measures) using sophisticated modelling procedures for open populations that are unavailable with all other indexing methods used for bats.
- If using radio-tracking, the fate of individual bats is known rather than extrapolated or inferred.
- Results from survival analyses can be used to help build predictive population models and for population viability analyses.

Disadvantages

Short-term monitoring using radio-transmitters

- By definition, inference about survival is limited because the studies are short term. The biggest problem is keeping transmitters attached for long enough to last through the desired monitoring operation. Although batteries in transmitters potentially last for 4 weeks, in reality transmitters rarely stay attached for longer than 2 weeks (maximum 1 month).

- If all bats in a small sample remain alive throughout the sampling period, resulting in apparent survival estimates of 1.0 (100% survival) across the sampling interval, then survival may be overestimated when extrapolating such statistics to the long term. Examination of the lower bound of the confidence intervals may provide a more realistic estimate if short-term estimates are generalised. Thus, the procedure is more suitable for comparing treatments where mortality does occur, and at differential rates.
- Sample size may be too small to extrapolate results to the total population.
- Individuals or age and sex classes selected for radio-tracking may not behave typically compared with all bats (e.g. an individual may not regularly forage and roost in the area where poison bait has been laid).

Long-term monitoring using permanent marks

- Mark-recapture studies are labour-intensive and expensive. They require a long time series and data on many individuals before reliable estimates of survival can be generated. Lebreton et al. (1992) recommended a minimum of five capture sessions for a study, but this will depend on the probability of recapturing animals. For long-tailed bats, we have found that > 10 years of data are required.
- The methods are dependent on being able to locate roost sites when necessary and catch sufficient numbers of bats quickly and humanely.
- Large sample sizes are needed to ensure recapture probabilities are high, but it is sometimes hard to catch a lot of bats in a reasonable number of capture sessions. Obtaining sufficient samples is virtually impossible if catching bats on their foraging grounds, which is why we recommend basing this method on captures at roost sites.
- Bats are disturbed by catching, handling and applying marks, and currently, they have to be subsequently recaptured. Thus, caution and care are needed when catching animals. Guidelines on ethical and best practice must be strictly adhered to.
- Analyses are sophisticated and require advice from experienced statisticians.
- Violations of model assumptions can cause problems when analysing data. Issues include transience effects where there is permanent emigration from the study site after first capture, and ‘trap-happiness’ or ‘trap-shyness’. Instantaneous samples are rarely possible in studies of bats because not enough recaptures are made in single capture sessions. However, this problem is generally minimised by standardising the sampling time and making it as short as possible so that the study population is ‘closed’ during the sampling period.

Suitability for inventory

Estimating survival is not recommended for undertaking an inventory of bats.

Suitability for monitoring

Mark-recapture of permanently marked long-tailed bats is the most robust technique for long-term monitoring of survival of this species provided all assumptions can be met and sufficient resources are available for a long-term study. Survival estimation is potentially suitable for lesser short-tailed bats now that it is possible to use transponders (PIT tags) with this species (Sedgeley & O'Donnell 2006, 2007).

Radio-tracking generally has limited value as a monitoring technique because tracking periods are relatively short and usually involve a small proportion of the population. However, the technique suits short-term management operations because the fate of individual bats is known rather than extrapolated or inferred, and results can be used to report on minimum number alive after the management operation or to calculate probabilities of survival.

Skills

In addition to marking and recapturing / resighting bats at roosts, workers require skills to find roosts if locations of occupied roosts in an area are not already known.

Skills required for finding roosts

Workers must be able to:

- Demonstrate a basic level of bushcraft.
- Identify areas of bat activity by using bat detectors to survey for bat calls. See 'Bats: counting away from roosts—bat detectors on line transects' (docdm-590701), and 'Bats: counting away from roosts—automatic bat detectors' (docdm-590733) for more information.
- Set up harp traps or construct mist net rigs in areas of bat activity. Training may be needed to learn how and where to place traps to optimise capture rates.
- Handle bats competently and humanely; identify, age, sex and measure them; and apply transmitters.
- Meet minimum standards—anyone wishing to catch and handle bats must receive appropriate training and must meet the minimum requirements for catching, handling, examining, measuring, and releasing bats described in the 'DOC best practice manual of conservation techniques for bats' (docdm-131465).
- Use radio-tracking to follow tagged bats and locate their communal roosts.

Skills required for using mark-recapture at roosts

For this approach, workers must be able to:

- Set up harp traps at tree roosts or caves using appropriate catching methods. Training may be needed to learn how and where to place traps to optimise capture rates.

- Handle bats competently and humanely; identify, age, sex and measure bats; and apply temporary and/or permanent marks (bands, radio transmitters and transponders).
- Meet minimum standards. Anyone wishing to catch and handle bats must receive appropriate training and must meet the minimum requirements described in the 'DOC best practice manual of conservation techniques for bats' (docdm-131465). At the time of writing, the DOC Animal Ethics Committee had only approved two people for injecting transponders into lesser short-tailed bats.
- Apply some statistical experience, and have experience with using computers and running computer programs.
- Identify violations of assumptions and the consequences of these on precision of the results.
- Get advice from a specialist statistician.

Resources

Trapping and mark-recapture methods are very expensive in terms of equipment and time:

- Intensive effort is required to locate the roosts. Preliminary surveys using bat detectors may be needed to find locations where bats are present.
- Radio-tracking bats is resource intensive, requiring mist nets and/or harp traps for catching bats, ropes to rig nets, transmitters, glue, scissors, antennae, receivers and a vehicle. Radio transmitters (c. $200/tag) and radio-tracking equipment (radio receivers and antennae, c. $3000/unit) are required. Personnel costs can be high when monitoring daily survival of radio-tagged bats as the minimum survey period is 2 weeks (and most surveys go for longer).
- Trapping bats also requires considerable resources in terms of equipment and time required to set up and run the traps. Equipment includes traps, ropes and strings, line-shooting and tree-climbing equipment, infrared video equipment, good spotlights and spare batteries.
- Equipment for marking and processing bats varies depending on the marking method. Holding bags, callipers, Pesola balances, fur-trimmers, clipboards, recording sheets and headlamps are relatively inexpensive. Long-tailed bat bands are also inexpensive, but transponders are more expensive (c. $10 each; injector gun c. $250; transponder reader > $250).
- You need a reasonably large pool of skilled workers to handle and mark bats, especially if large samples are sought for use in calculating tagging ratios.
- Automatic transponder readers will be quite inexpensive (c. $250 per unit), but units will be required for perhaps 10–20 roost trees and personnel costs will be high if trees need to be climbed and readers maintained regularly.

Minimum attributes

Consistent measurement and recording of these attributes is critical for the implementation of the method. Other attributes may be optional depending on your objective. For more information refer to 'Full details of technique and best practice'.

DOC staff must complete a 'Standard inventory and monitoring project plan' (docdm-146272).

Minimum attributes to record:

- Date
- Location of trapping session
- Where trapped (roost number)
- Weather
- Observer
- Whether a bat was a 'recapture' or an untagged bat
- Band or transponder tag number, or location of fur clip on body
- Age, sex and reproductive class of all bats caught
- Numbers of bats present at the roost on the night bats were captured, and the number caught

Record field observations on a paper form (see 'Bat specimen record form'—docdm-141173), then store data in a computer-based spreadsheet.

If using radio-tagging, also record:

- Radio-tag frequency/channel number on receiver
- The dates and total number of days over which the transmitter is functional
- Total time (period) monitored (dates and number of days)
- The proportion of the total time monitored that the bat was active
- The fate of the bat (whether alive or dead)
- Appropriate covariates (e.g. treatment or non-treatment)

Data storage

Forward copies of completed survey sheets to the survey administrator, or enter data into an appropriate spreadsheet as soon as possible. Collate, consolidate and store survey information securely, also as soon as possible, and preferably immediately on return from the field. The key steps here are data entry, storage and maintenance for later analysis, followed by copying and data backup for security.

Summarise the results in a spreadsheet or equivalent. Arrange data as 'column variables', i.e. arrange data from each field on the data sheet (date, time, location, plot designation, number seen, identity, etc.) in columns, with each row representing the occasion on which a given survey plot was sampled. Columns in the spreadsheet should include all data recorded on the original field sheet because the influences of factors such as location, observer, weather, etc. need to be accounted for in future analyses.

If data storage is designed well at the outset, it will make the job of analysis and interpretation much easier. Before storing data, check for missing information and errors, and ensure metadata are recorded.

Storage tools can be either manual or electronic systems (or both, preferably). They will usually be summary sheets, other physical filing systems, or electronic spreadsheets and databases. Use appropriate file formats such as .xls, .txt, .dbf or specific analysis software formats. Copy and/or backup all data, whether electronic, data sheets, metadata or site access descriptions, preferably offline if the primary storage location is part of a networked system. Store the copy at a separate location for security purposes.

Analysis, interpretation and reporting

Seek statistical advice from a biometrician or suitably experienced person prior to undertaking any analysis.

This method measures:

- Estimates of apparent survival
- Estimates of recapture probability

Short-term monitoring using radio-transmitters

The simplest analysis is the number alive or proportion of bats that survived a management operation. If survival estimates are calculated using short-term radio-tracking data (e.g. Kaplan-Meier Method or Mayfield Method), caution must be used when extrapolating such statistics to the long term so that survival estimates are not over-inflated. Examination of the lower bound of the confidence intervals may provide a more realistic estimate if short-term estimates are generalised. Thus, the procedure is more suitable for comparing treatments where mortality does occur, and at differential rates. See Robertson & Westbrooke (2005) for further details.

Long-term monitoring using permanent marks

Results should be entered into a spreadsheet. The format required will depend on the statistical model used for the analysis but will consist of a list of all animals marked and a series of ones and zeros for whether they were sighted again over regular time intervals (a capture history; see Table 1 in 'Case study A'). In many cases, program MARK will provide all the analysis options required for estimating apparent survival in open populations. Analysing data from mark-recapture studies of open populations is flexible but more complicated. Conclusions about birth, death, immigration or emigration may be confounded by our limited ability to detect these processes. Extra parameters are needed to account for animals entering and leaving the population.

Data from a mark-recapture study with several capture sessions will give two types of information:

1. The rate at which animals are recaptured

2. The ratio of marked to unmarked animals captured each session

The recapture rate (1) is used for the calculation of survival estimates, while data from both (1) and (2) are necessary to estimate population size (Pollock et al. 1990). Analysis of mark-recapture data involves building and testing models, usually with the aid of an appropriate computer software program.

Within MARK, each analysis method will have its own specialised format; this should be considered at the start of the study so information can be collected accordingly. Data can be collected in Excel (Table 1), then saved as an '.inp' file so it can be accessed using MARK. This program allows models to be created and run to produce survival and recapture estimates. Full details of this type of analysis are found in Pryde (2003).

Case study A

Case study A: modelling survivorship in long-tailed bats using the computer program MARK

Synopsis

The long-tailed bat (*Chalinolobus tuberculatus*) is a rainforest specialist that roosts in tree cavities, switching to a new roost site virtually every day (O'Donnell & Sedgeley 2006). It is classed as threatened, but the rate of decline was unknown when the recovery programme for this species commenced (Molloy 1995). A worked example of using MARK for estimating the survival of long-tailed bats was developed by Pryde (2003) and Pryde et al. (2005). See Pryde (2003) for full details.

Objectives

The primary hypothesis investigated was that survival rates of long-tailed bats would vary with time and be dependent on levels of introduced predators which prey on cavity-breeding wildlife in New Zealand.

Sampling design and methods

The long-tailed bat breeding season is highly synchronised, with a single baby produced each year. Female bats tend to congregate in maternity roosts to raise young during November–February (O'Donnell 2002). In this 10-year study, bats were caught and banded from a random sample (< 10%) of > 400 known roost sites using harp traps (Sedgeley & O'Donnell 1996) during January and February of each year when young of the year began flying. Consistent methods were used over a 10-year study period to catch and mark bats with 2.9 mm flanged bat bands (from The Mammal Society, UK) (*n* = 5286 captures, representing 1026 individuals).

Table 1. Example of an Excel spreadsheet for entering and coding mark-recapture data (see 'Developing a capture history').

Year			94	95	96	97	98	99	00	01	02	03	Encounter history				
Band No.														AM	JM	AF	JF
2070560	J	M	0	1	1	0	0	0	0	0	0	0	0110000000	0	1	0	0
2070559	J	F	0	1	1	0	0	0	0	0	0	0	0110000000	0	0	0	1
110510	A	M	0	1	0	0	0	0	1	0	0	0	0100001000	1	0	0	0
110509	A	F	0	1	0	0	0	0	0	0	0	0	0100000000	0	0	1	0
110508	A	M	0	1	0	0	0	0	0	0	0	0	0100000000	1	0	0	0
110507	A	M	0	1	0	0	0	0	0	0	0	0	0100000000	1	0	0	0
110506	A	F	1	1	1	1	1	1	0	0	0	0	1111110000	0	0	1	0
110505	A	F	1	1	0	0	0	0	0	0	0	0	1100000000	0	0	1	0
110504	A	F	0	1	1	0	0	0	0	0	0	0	0110000000	0	0	1	0
110503	A	F	0	1	0	0	0	0	0	0	0	0	0100000000	0	0	1	0

AM = Adult male, JM = Juvenile male, AF = Adult female, JF = Juvenile female

Results

Developing a capture history

The format of data required for the analysis software, MARK, is the 'encounter history'. This is a series of ones and zeros that show whether or not a long-tailed bat was trapped or seen during each capture session. In this study, data from within a summer catching period were pooled into one capture occasion per year, and capture histories were constructed for ten occasions in the years 1993–2003. For example, an individual bat caught in the 1st year (coded '1'), not in the following 3 years (coded '0'), again in the 5th year and 7th year, but not in the 6th, 8th or 9th year, would have an encounter history of '100010100'.

These encounter histories can have specifiers for age, sex and band number added to them (as in Table 1).

The file format used for analysis using MARK, an '.inp' file, looks like this:

```
/* 2070560 */   0110000000   0 1 0 0;
/* 2070559 */   0110000000   0 0 0 1;
/* 110510 */    0100001000   1 0 0 0;
/* 110509 */    0100000000   0 0 1 0;
/* 110508 */    0100000000   1 0 0 0;
/* 110507 */    0100000000   1 0 0 0;
/* 110506 */    1111110000   0 0 1 0;
/* 110505 */    1100000000   0 0 1 0;
/* 110504 */    0110000000   0 0 1 0;
/* 110503 */    0100000000   0 0 1 0;
```

Applying the Cormack-Jolly-Seber (CJS) model: the CJS model ('recapture only' option) within MARK 3.0 was used to model factors influencing variation in apparent over-winter survival (standard notation =) and probability of recapture (*p*), including the influences of sex (*s*), age (*a*), sub-population (*g*), time effects (*t* = year), winter temperatures and density of predators. The global model (one that includes all the parameters thought to be important to survival) was therefore defined using standard notation as:

(*s***a***g***t*) *p* (*s***a***g***t*)

The global model and a range of alternative models were run using the sine link for interactive models and the design matrix with the logit function for additive models (Cooch & White 2004).

Departure of the data from the underlying assumptions of the model was tested using the parametric bootstrapping Goodness of Fit method available in MARK. The Goodness of Fit test for the global model showed that the data were mildly over-dispersed, indicating that assumptions 1 and 2 of the CJS model (see 'Assumptions') may have been violated, as is often the case for data on bats. Therefore, data were adjusted for over-dispersion ($\hat{c}$) by adjusting the variance-inflation factor within MARK (Cooch & White 2004).

Model selection was based on the Quasi Akaike's Information Criterion, corrected for over-dispersion using the $\hat{c}$ adjustment and small sample size bias (*c*) (QAICc) (Anderson et al. 1998; Burnham & Anderson 2002). QAICc uses an information theoretic approach to allow selection of the most parsimonious model from a series of candidate models, where the best model is the one with the lowest QAICc. Model selection using QAICc seeks to achieve a compromise between model fit (likelihood) and simplicity (measured by the number of parameters). Increasing the number of parameters in the model reduces the precision of the estimates and therefore the reliability of inference. However, an overly simplified model also results in unreliable inference.

The difference in QAICc (ΔQAICc) between each model and the model with the smallest observed QAICc from the set of models considered (i.e. the 'best-fit' model) was calculated along with the Akaike weight for each model. The bigger the ΔQAICc compared with the best model, the smaller the weight and the less plausible the alternative model. Burnham & Anderson (2002) suggest as an approximate guide that models with ΔQAICc < 2 should be considered to have substantial support and thus used for making inferences. Models having ΔQAICc of about 4 to 7 when compared with the best-fit model have considerably less support, and models with ΔQAICc > 10 essentially have no support. Akaike weights are proportional to the relative likelihood of each model and are useful in suggesting the weight of evidence in favour of any given model being the actual best model in the set.

In the case of the New Zealand long-tailed bat, the probability of recapture (*p*) varied with social group, time, sex and age (Table 2) (Pryde et al. 2005). Females had a higher recapture rate (range = 0.58–0.95) than males (range = 0.17–0.82). Juvenile recapture rate (0.18–0.95) was comparable to that of adults (range = 0.17–0.97). All six factors influenced survival (social group, year, sex, age, predators and over-winter temperature). Four additive models clearly described survival parameters better than the global model, with models 1 and 2 having the greatest weight (*w*) (Table 2). Both models 1 and 2 indicated that survival was lower in years with high predator numbers. Although there was evidence that high over-winter temperatures reduced survival (Model 1), this effect was not compelling, as shown by the small ΔQAICc value between models 1 and 2 and a minor difference in the likelihood ratio test (χ^2 =

2.97, *df* = 1, *p* = 0.08). Therefore, model averaging (Cooch & White 2004) was undertaken to account for the weightings of each model. Average annual survival rates ranged from 0.52–0.83 per year for females (Fig. 1) and 0.34–0.69 for males. Survival was higher for females than for males, higher for adults than for juveniles, and lower in years where introduced predator numbers were high (1996, 2000, 2001) (Pryde et al. 2005).

Limitations and points to consider

In the study, two factors influenced the precision of the survival estimates and the level of inference of our models. First, the capture period varied among years. In the first 3 years it was over 5 months, whereas for the majority of the study it was 2 months. The number of new captures of adult bats steadily increased over the first 3 years of the study, but few new adults were caught after that. In subsequent years, the majority of adults caught were already marked, and new captures were generally young of the year. Although the study could have been improved if the sampling time had been standardised and as short as possible (Smith & Anderson 1987), the variable sample periods are acceptable because there was relatively low mortality during the sampling periods themselves (Hargrove & Borland 1994). The second factor influencing precision was that female bats were caught at maternity colonies where they congregate with the young; therefore captures of adults were not independent. Over-dispersion adjustments were made to these data to account for lack of independence in captures of adults, resulting in inflated variances, which reduced the overall level of inference achievable (Pollock et al. 1990).

The probability of survival was found to vary with social group, sex and age. It was also found to vary with the level of introduced predators—in years with high numbers of introduced predators (compared with ‘low predator years’), survival was found to be lower. In this example, years 1996, 2000 and 2001 were ‘high predator years’ due to beech masting in the previous year. Using these survival figures for high and low predator years, combined with annual productivity rates, in a survival matrix gave a population growth rate for these two scenarios. If the frequency of high predator years continues at the current rate of 3 out of 10 years, there is a high probability of extinction of long-tailed bats in the Eglinton Valley in 50 years. If there is effective predator control in the high predator years, extinction can be averted (Fig. 2).

Table 2. The top four ranked models along with the original global model (No. 5) describing factors affecting survival and recapture probability of long-tailed bats in the Eglinton Valley, New Zealand, using MARK. The models use standard notation: ϕ = apparent survival; *p* = recapture; with the variables *g* = sub-population (1, 2, 3); *a* = age (juvenile, adult); *t* = time; *s* = sex (male, female); *pred* = predator levels; *temp* = mean over-winter temperature. Statistics include Quasi Akaike's Information Criterion (QAICc, adjusted for small sample sizes); differences in QAICc (ΔQAICc); Akaike's weight (*w*); number of parameters (*np*); and deviance (Qdev).

	Model	QAICc	ΔQAICc	*w*	*np*	Qdev
1.	ϕ (*g+a+s+pred+temp*) *p*(*g+a+s+t*)	2373.85	0	0.61	20	779.41
2.	ϕ (*g+a+s+pred*) *p*(*g+a+s+t*)	2374.78	0.93	0.38	19	782.39
3.	ϕ (*g+a+s+t*) *p(g+a+s+t*)	2382.82	8.97	0.01	26	776.07
4.	ϕ (*g+a+s+temp*) *p*(*g+a+s+t*)	2410.07	36.22	0	19	817.68
5.	ϕ (*g*a*s*t*) *p*(*g*a*s*t*)	2539.87	166.02	0	186	572.46

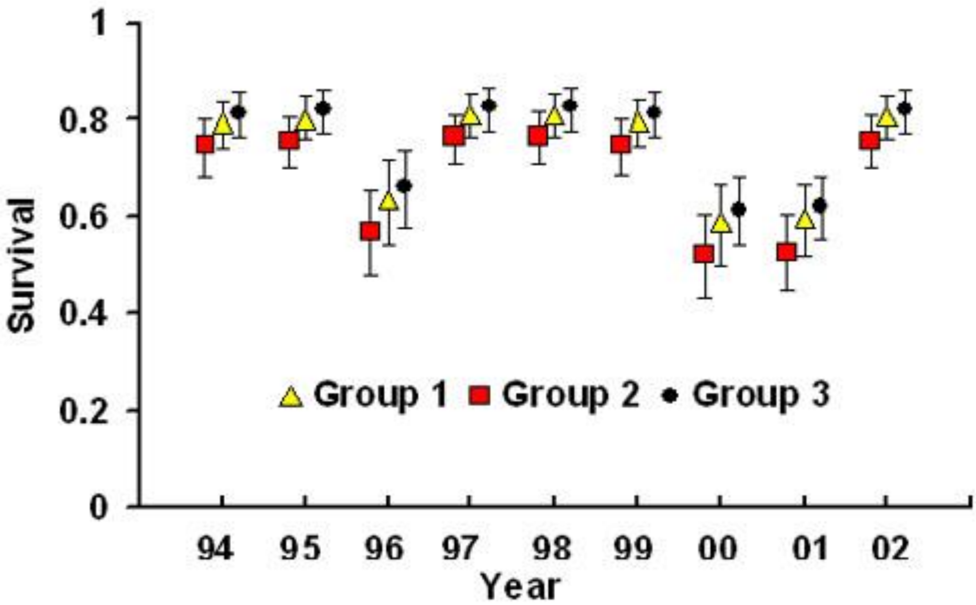

Figure 1. Model average annual over-winter survival (± SE) of female long-tailed bats from three sub-populations (Groups 1–3) in the Eglinton Valley, New Zealand, from 1993 to 2003.

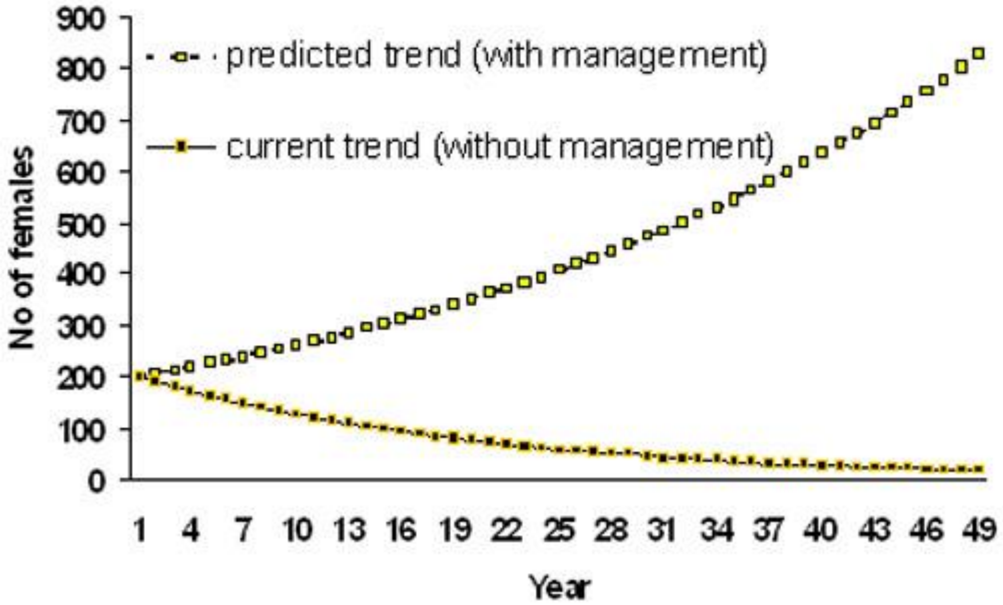

Figure 2. Predicted population trends in long-tailed bats with and without control of introduced predators. (Simulation based on matrix modelling; Pryde et al. 2005.)

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Case study B

Case study B: simple analysis of the fate of lesser short-tailed bats during a rat eradication (poison) programme on Codfish Island/Whenua Hou

Synopsis

Introduced Pacific rats (*Rattus exulans*) were eradicated from Codfish Island during winter 1998 following two applications of toxic baits containing the anti-coagulant poison brodifacoum. One of the methods used to assess potential impact of the poison on a population of lesser short-tailed bats was to monitor the fate of radio-tagged bats throughout the poisoning operation. Eight wild bats were monitored during the pre-poisoning period and 11 in the period when poison lay on the ground. Each bat was followed for an average of 12 days. All bats were active on most nights, and all were alive at the time their transmitters failed (Sedgeley & Anderson 2000). Assuming that the behaviour of the 19 bats monitored was representative of the population of lesser short-tailed bats on Codfish Island, Sedgeley & Anderson (2000) concluded that the poison operation did not adversely affect the bats.

Case study C

Case study C: analysing radio-tracking survivorship data using Mayfield or Kaplan-Meier methods

The authors are not aware of any case studies using the Mayfield or Kaplan-Meier methods for bats. However, the publication by Robertson & Westbrooke (2005)[1] gives examples of different survivorship estimates from ongoing and past studies of two bird species (brown kiwi, *Apteryx mantelli*; and kererū, *Hemiphaga novaeseelandiae*). They provide a sample Excel spreadsheet for the storage of raw data

[1] Available at: http://www.doc.govt.nz/upload/documents/science-and-technical/docts31.pdf

and for processing and transferring them to the SPSS statistical package to carry out survival analysis. They also provide worked examples in Excel for the calculation of survivorship rate using simple methods and examples in both Excel and SPSS for the Kaplan-Meier method, and for testing differences in survival between two or more groups of individuals using a log-rank (Mantel-Haenszel) test.

Full details of technique and best practice

Setting objectives

Our understanding of the population dynamics and survivorship of bats is likely to increase exponentially over the coming decades as bat ecologists abandon traditional sample methods, improve sampling and design strategies, use smaller radio transmitters, and begin using probabilistic survivorship models as a matter of course. The bat researcher should follow the following steps when considering undertaking studies of survivorship:

1. Define clear questions and objectives and assess whether mark-recapture and survival analyses might be appropriate to answer the questions.
2. Obtain a basic understanding of the ecology of the bat species in question. A pilot study may be appropriate in species that are poorly known.
3. Develop a basic understanding of mark-recapture and survival analyses, their underlying assumptions and limitations.
4. Determine whether permanent, individual marks can be applied humanely to the species of bat in question.
5. Given steps 1 to 4 above, assess whether mark-recapture or survival analyses are appropriate. Ideally, studies should be long term. Good sample sizes need to be achievable (to ensure high recapture probabilities), recaptures should be unbiased, and appropriate covariates collected.

Choosing appropriate methods for marking

Mark-recapture studies are dependent on being able to apply recognisable marks to bats that last for the duration of the study. Marks must be applied ethically and humanely. Permanent marks that require recapture and re-handling of bats include forearm bands for long-tailed bats only, and PIT tags for lesser short-tailed bats. Transponders show great promise as a marking technique because bats can be ‘recaptured’ without re-handling using automatic transponder readers located at a representative number of roost entrances to ensure high recapture probabilities. Radio-transmitters are only suitable for short-term studies.

Trapping and handling methods

Full details of best practice for trapping, capturing, handling, marking and tracking bats are described in the ‘DOC best practice manual of conservation techniques for bats’ (docdm-131465). Catching bats using harp traps or mist nests on bat foraging grounds is appropriate if radio-transmitters are the main marking method. If large samples of individually marked bats are required, a suitable colonial roost needs to be found using radio-tracking. A suitable roost is one in which all young have become independent, and the entrance is in a position on a tree where lines can be hoisted and the trap raised without being caught on the tree or disturbing the bats. A trap is positioned in front of a roost exit with the catch bag about 30 cm below the entrance. Bats are caught as they emerge at dusk. Once the trap is lowered, bats can be placed directly into cloth holding bags, and then processed.

Now that lesser short-tailed bats have been tagged successfully using transponders inserted under the skin, and preliminary trials using automatic tag readers and data loggers positioned at the roost hole have been successful at recording the number of bats with tags exiting the roost, it may not be necessary to physically recapture bats with transponders in the future (Sedgeley & O'Donnell 2006, 2007). However, initial capture sessions (to insert transponders in the first instance) will need to follow the same protocols outlined above.

Minimising disturbance

Bats are disturbed by catching, handling and applying marks, and they have to be recaptured subsequently. Thus, caution and care need to be used when catching animals. In the Eglinton Valley, there is no evidence that catching bats at their roosts causes them to abandon a tree if best practice is strictly adhered to (Sedgeley & O'Donnell 1996). However, some bat species overseas are known to abandon their roosts if disturbed. Some lesser short-tailed bat colonies number several thousand individuals. It is inappropriate and unnecessary to catch all bats in such roosts. Roosts must not be trapped during periods when there are dependent young present in the colonies. This ensures lactating females can feed their young without disturbance and avoids the risk of females abandoning their young.

Selecting an appropriate technique

Practitioners should consider the objectives of their study, the degree of precision they require, the resources available, the behaviour of their study animal, and whether the assumptions of analysis models can be met.

Open-population models estimate probability of survival (apparent survival, ϕ) and probability of recapture (*p*), with parameters for different time periods represented as follows:

Time period	1	2	3	4	5	6	7	8	9
Survival	f1	f2	f3	f4	f5	f6	f7	f8	
Recapture	p1	p2	p3	p4	p5	p6	p7	p8	

'Apparent' survival (1–ϕ) does not distinguish between emigration and death but is defined as the probability of a bat surviving from one year to the next and remaining in the study population. Estimates of apparent survival are likely to be underestimates of true survival because some bats almost certainly emigrate from populations (Hoyle et al. 2001).

Bats in any survey session can be divided into three categories:

1. Live animals that are seen
2. Live animals that are not seen
3. Dead animals (Lettink & Armstrong 2003)

If individuals tended to be captured in most sessions and 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. Estimating the relative proportions in these two categories can be undertaken using open models, the most commonly used being the Cormack-Jolly-Seber (CJS) model (Lebreton et al. 1992). Open models such as the CJS model, although more problematic for estimating population size, can be used to estimate survival, recruitment and population growth (Thompson et al. 1998). Other options include the simpler Jolly-Seber model, Pradel models, and recovery models for marked animals that are found dead. Such models are appropriate for open populations, i.e. those subject to birth, death, immigration and emigration during a study. Others are the 'Heterogeneity' model, the 'Trap Response' model, and the 'Time' model, all of which can cope with variation in capture probabilities in closed populations over time (Otis et al. 1978) and DENSITY, a 'spatially explicit capture-recapture model', which takes into account edge effects (Efford et al. 2004). The mathematical theory underlying open-population mark-recapture models is described by Pollock et al. (1990).

Estimating survival using program MARK

Program MARK is arguably the most comprehensive software available for mark-recapture analysis at the time of writing. It amalgamates much of the existing knowledge for estimating population parameters from marked animals into one computer program. It has increased the power and accessibility of mark-recapture analysis and is particularly good for estimating survival (White & Burnham 1999). MARK largely supersedes a range of programs. It allows estimation of survival rates and, to a lesser degree, population size by fitting a series of powerful statistical models to mark-recapture data. Marked animals can be re-encountered live or dead. MARK can run analyses from recovery and recapture (open- and closed-population) data, or from a combination of both. Version 3.0 supports 26 categories of analysis models including CJS, dead animal recoveries, 'known fate' for use with radio telemetry data, Pradel models and a range of robust designs. Individual covariates are permitted, and the use of age-structured models is possible. As new advances are made in mark-recapture methods, they are added to the program. 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 (see Lettink & Armstrong 2003 for a summary).

MARK allows models to be created and run using an intuitive Windows-based interface. Although the program is much easier to operate than previous programs, it is complex and by no means trivial to use. It requires careful attention to formulating questions, assessing assumptions, organising data, and using relevant models. Attending a MARK training course is immensely valuable. Most people should also seek advice from an experienced statistician.

MARK can be downloaded free-of-charge from the MARK website[2]. There is extensive online support available when learning the program. The standard reference is White & Burnham (1999), and a draft version of this publication is available on the MARK website. Cooch & White have written a guidebook titled 'Using MARK—a gentle introduction'. This can also be downloaded from the MARK website (Cooch & White 2004). There is an interactive website devoted to questions and answers about MARK. A working example of using MARK for the threatened New Zealand long-tailed bat was developed by Pryde (2003) and Pryde et al. (2005). Full details of the steps required to undertake this type of analysis are found in Pryde (2003).

Estimates of survival from radio-tracking

This method is most likely to be used for monitoring survival through management operations (e.g. to determine whether adult female bats survive through a 1080 drop). Bats are trapped on foraging grounds or at roost sites and radio-transmitters are attached to a relatively large sample (> 20) of bats. Sampling could either focus on individuals that are representative of a range of sex and age classes, or concentrate on one group to answer a specific question. At a minimum, bats should be radio-tracked through the crucial phases of the management operation. The number of radio-tagged bats surviving the operation can be used simply to report on minimum number alive (and proportion), or to calculate probabilities of survival.

There is a wealth of techniques for analysing survival based on radio-telemetry data. Comprehensive reviews can be found in Bunck et al. (1995), White & Garrott (1990) and Winterstein et al. (2001). The four most common analysis methods are:

1. Simple descriptive statistics such as number alive (and proportion) following management.
2. Mayfield method. This method and its derivatives for analysing nesting success in birds are often extended to radio-tracking data (Heisey & Fuller 1985). This is a simple approximation of mortality, obtained by dividing the number of deaths (*d*) by the total time (*t*) that animals have carried active transmitters. The method assumes constant survival which, in bats, is likely to be unrealistic. Nevertheless, derivatives of the Mayfield method remain useful if its assumptions are met (Winterstein et al. 2001).
3. Kaplan-Meier method. When the assumption of constant survival cannot be made, which is likely for most studies of bats, the nonparametric Kaplan-Meier method (also known as the Kaplan-Meier procedure) is more appropriate (Bunck et al. 1995). This procedure is a method for estimating survival in the presence of censored cases where there is some mortality. It does not require specific assumptions about the distribution of survival times. Censored cases are cases for which timing of the second event (death) is not recorded. In the case of radio-tracking data, a proportion of bats are likely to still be alive at the end of the study while others might have disappeared. The Kaplan-Meier model is based on estimating conditional probabilities at each time point when an event occurs, and then estimating the survival rate at each point in time. The relatively recent developments in the use of radio-tracking to study bats potentially allow accurate measurement of survivorship without many of the mathematical problems associated with mark-recapture analysis (Robertson & Westbrooke 2005). Survival estimates for

[2] http://www.phidot.org/software/mark/

long-tailed bats and lesser short-tailed bats are limited to short-term estimates because transmitters remain attached for relatively short times (daily, weekly or monthly survival rates). Short-term survival rate estimates can be modified mathematically (for the purpose of extrapolating to a more meaningful time frame) by raising the survival rate by an appropriate power (Robertson & Westbrooke 2005). For example, a monthly survival of 0.90 equates to an annual survival of 0.9012 = 0.28. However, such extrapolation should be avoided because it assumes constant survival and subtle variations in the short-term estimate influence average annual survival estimates considerably.

The Kaplan-Meier method is available in most comprehensive statistical software packages or can be formulated in an Excel spreadsheet using tag number, age and sex variables, the time the transmitter was active for, total tracking period and fate (whether alive or dead) and appropriate covariates (Robertson & Westbrooke 2005). In the statistical package SPSS, cumulative survival functions (± errors) are tabulated or graphed over time and it is possible to compare survivorship in two or more groups (e.g. males v. females, etc.). The standard test for comparing groups is the nonparametric Mantel-Haentszel test, although SPSS supports other options as well. The Mantel-Haentszel test is a log-rank test with a distribution approximating a χ^2 distribution with $g - 1$ degrees of freedom for comparing survival between two or more groups (g) of individuals. It tests the hypothesis that the time of death in the groups is significantly different from that which would occur randomly.

4. ‘Known fate’ model. This model, available in program MARK (White & Burnham 1999), also has the facilities to analyse data from radio-telemetry studies. The ‘known fate’ model looks at survival over discrete time periods. It has advantages in some situations, such as those where data is missing.

Estimating population growth rate

In recent years, there has been progressively less emphasis on estimating abundance and progressively more emphasis on estimating population growth or lambda (λ) (Lettink & Armstrong 2003). 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 ($\lambda < 1.0$). Separate estimates of survival and recruitment can be combined to estimate λ. However, λ can also be estimated directly from either the Jolly-Seber (JS) model or Pradel’s (1996) model (which is also available in MARK). Unlike the JS, Pradel’s model does not estimate abundance or estimate separate capture and recapture probabilities. Its assumptions are otherwise similar to those of the JS model.

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Appendix A

The following Department of Conservation documents are referred to in this method:

docdm-141173	Bat specimen record form
docdm-590733	Bats: counting away from roosts—automatic bat detectors
docdm-590701	Bats: counting away from roosts—bat detectors on line transects
docdm-131465	DOC best practice manual of conservation techniques for bats
docdm-146272	Standard inventory and monitoring project plan