Using Program 'MARK' for assessing survival in cryptic threatened species

Case study using long-tailed bats (*Chalinolobus tuberculatus*)

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ABSTRACT

Program MARK is a sophisticated computer program that can analyse mark-recapture data and produce survival and population estimates which can then be used in a population viability analysis. The ability to detect trends in survival and population size over time enables conservation managers to make good decisions in species management. This report is a step-by-step guide to the basics of the MARK program using an analysis of long-tailed bat (*Chalinolobus tuberculatus*) data as a case study. It is intended as a template to encourage more conservation managers to apply these techniques to monitoring threatened species. It is designed to be used in-conjunction with the MARK users' guide. Analyses using MARK can quickly become complicated, so expert advice should be sought before using it.

Keywords: mark-recapture, long-tailed bat, survival, MARK, threatened species, population estimates, *Chalinolobus tuberculatus*

1. Introduction

1.1 WHY USE MARK-RECAPTURE STUDIES?

Habitat alteration, introduced predators and competition continue to have adverse effects on the fauna of New Zealand (King 1990). As a result, monitoring biological populations has become increasingly important. Assessing risk to populations can be done through a **population viability analysis**[1]. This relies on estimating vital rates (e.g. survival and reproduction) for the **population** that can often only be obtained using mark-recapture studies (White & Burnham 1999). By monitoring and analysing data from sub-populations managers can incorporate the results of mark-recapture studies into their adaptive management of populations (White & Burnham 1999).

Mark-recapture studies are useful for any population where animals can be individually marked, and are particularly useful for populations where animals cannot be consistently found. Such studies allow estimation of the population **parameters** after catching and marking a proportion of the population, releasing them, and re-sampling on one or more occasions. Mark-recapture studies can be used on **closed** and **open populations**. Closed models such as the Peterson-Lincoln estimate (Seber 1982) rely on no births, deaths, immigration or emigration during the sampling period, and can only be used to estimate population size at one point in time. Open models such as the Cormack-Jolly-Seber (CJS), although more problematic for estimating population size, can be used to estimate survival, recruitment and population growth (see Lettink & Armstrong 2003: this volume for more detailed information).

1.2 WHY USE THE COMPUTER PROGRAM MARK?

Program MARK[2], developed by Gary White at Colorado State University, has increased the power and accessibility of mark-recapture analysis in recent years. It was developed to amalgamate the existing knowledge into one computer program that can estimate population parameters from marked animals. It allows estimation of survival rates and population size by fitting a series of powerful statistical models to mark-recapture data. Marked animals can be re-encountered live or dead. The program is particularly good for estimating survival (White & Burnham 1999). Lettink & Armstrong 2003: this volume have reviewed other methods of measuring survival and abundance.

1.3 THE PROBLEMS ASSOCIATED WITH MONITORING POPULATIONS OF BATS AND OTHER CRYPTIC SPECIES

Effective species management relies on identifying the location and size of populations and establishing baseline measurements against which to measure future changes. Determining whether a population is increasing or decreasing

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[1]   Many of the terms used in this report are defined in the glossary of terms, Appendix 1, p. 62.

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

helps in prioritising management areas. Monitoring cryptic species such as bats is particularly difficult because only a small portion of the population may be detected in a survey and individuals are difficult to distinguish due to their rarity, patchy distribution and their nocturnal behaviour. Obtaining baseline measurements of distribution and abundance is therefore not straightforward. Data from a well-designed mark-recapture study, analysed using program MARK, can help assess survival rates and population trends over time in such species, so that managers can respond and management adapted appropriately.

1.4 CASE STUDY: LONG-TAILED BATS

The long-tailed bat (*Chalinolobus tuberculatus*) is one of two extant bat species in New Zealand. Distribution and abundance are considered to have declined significantly over the last 150 years and the species is currently classed as threatened (Molloy 1995; O'Donnell 2000a). There has been little progress towards determining the causes of the decline. Suggestions include loss of foraging and roosting habitat, predation by introduced mammals, competition for roost sites from introduced mammals, birds and wasps, use of toxins, and human interference and disturbance of roost sites (O'Donnell 2001). Presence or absence distribution maps have been produced throughout the 1900s, but few quantitative measures of the extent of the decline have been made (O'Donnell 2000a).

Advances in technology in the early 1990s have made the study of these cryptic animals viable (O'Donnell 2001). Equipment such as ultrasonic bat detectors, small transmitters, specialised harp traps and miniaturised infra-red cameras led to improved knowledge of behaviour, habitat use and distribution and made quantitative studies possible (O'Donnell & Sedgeley 1994; O'Donnell 2001).

Long-tailed bats have been studied over the last ten years in the Eglinton Valley, Fiordland. The research shows the study population of bats is divided into three distinct social groups. The foraging area of the social groups overlaps but roosts are in distinct areas, with only 1.6% of individuals switching between groups. Female bats tend to congregate in large maternity roosts to raise young in the breeding season (November–February). These communal roosts are largely composed of breeding females and their young, although some males (average of 15%) and non-breeding females (average of 22%) may be present. Bats shift to new roosts virtually every day and intermixing between members of the same social group is frequent. Adult females and their young are caught most often, whereas young females are rarely caught in communal roosts until they reappear when they are breeding one to two years after birth. Male bats tend to roost alone so are rarely caught (O'Donnell 2000b). This type of biological information is important in the design of a mark-recapture study because it helps in developing appropriate models (Burnham & Anderson 1998).

Bats were caught using harp traps (for details see O'Donnell & Sedgeley 1999). Trapping was carried out every summer (between November and February) from 1993 to 2003. Initially, harp traps were placed in areas likely to be used by bats, such as flight paths or foraging areas. Once a female or a juvenile bat was caught, a transmitter was attached and the bat radio-tracked to a roost. The roost was then harp-trapped and all the bats caught were fitted with small

aluminium forearm bands (O'Donnell & Sedgeley 1999). The forearm bands are individually numbered so that recaptures can be identified. Each social group was trapped several times throughout each summer season and a database of recaptures was accumulated over time.

2. Objectives

The aim of this report is to condense and simplify instructions for using what is essentially a complicated computer program. A realistic data-set of monitoring data for a population of long-tailed bats is used as a working example.

Specific objectives are to:
- provide a short step-by-step guide to the basics of Program MARK
- demonstrate the utility of MARK using the long-tailed bat database
- encourage more conservation managers to apply these techniques to monitoring threatened species

This report should be read alongside the more general introduction to using mark-recapture studies by Lettink & Armstrong, 2003: this volume. **It must also be realised that analyses using MARK can quickly become complicated, and expert advice should also be sought.**

3. Instructions for using Mark

The steps to analyse data using MARK are summarised in Box 1. The following section describes these steps in greater detail.
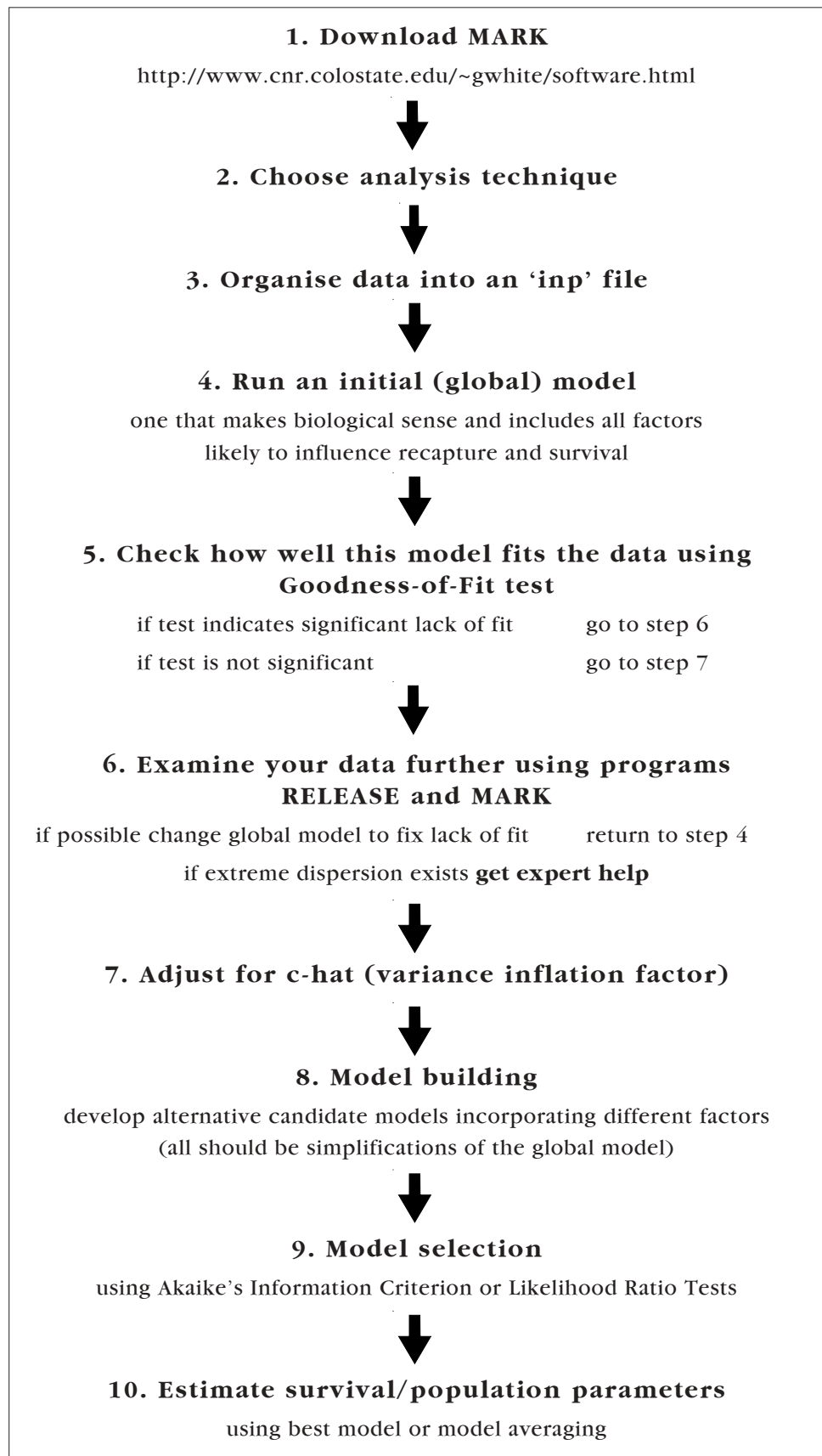
3.1 DOWNLOADING MARK

The main source for MARK is Gary White's website is:
http://www.cnr.colostate.edu/~gwhite/software.html
from which MARK can be downloaded. MARK is continually revised and updated, so it is advisable to download it frequently. The site contains a brief introduction to the program, details of recent changes and has links to other web-based resources. MARK is a WINDOWS-based program that needs a machine running windows 95, 98, NT, XP or better. Cooch & White (2001) recommend a pentium-based machine with 300 MHz or better and at least 64 Mb of RAM. To download, click on the downloading and installation tab and you will be asked where you want to download the setup.exe file. Running this file allows the installation of MARK with prompts as to where you want to install the program. The installation routine will place a shortcut to MARK on the desktop. For Department of Conservation readers, MARK is available via an MAC request form.

1. Download MARK

http://www.cnr.colostate.edu/~gwhite/software.html

↓

2. Choose analysis technique

↓

3. Organise data into an 'inp' file

↓

4. Run an initial (global) model

one that makes biological sense and includes all factors
likely to influence recapture and survival

↓

5. Check how well this model fits the data using Goodness-of-Fit test

if test indicates significant lack of fit   go to step 6

if test is not significant   go to step 7

↓

6. Examine your data further using programs RELEASE and MARK

if possible change global model to fix lack of fit   return to step 4

if extreme dispersion exists **get expert help**

↓

7. Adjust for c-hat (variance inflation factor)

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8. Model building

develop alternative candidate models incorporating different factors
(all should be simplifications of the global model)

↓

9. Model selection

using Akaike's Information Criterion or Likelihood Ratio Tests

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10. Estimate survival/population parameters

using best model or model averaging

Gary White's website also provides access and download facilities to an introductory users' guide to MARK called 'a Gentle Introduction' maintained by Evan Cooch (Cooch & White 2001). The guide provides detailed information on the program and should be read in conjunction with this document. It is a working document that is continually revised and updated.

There is a also a hypertext discussion program where people can email questions on the problems they are having with the program or particular analysis. This can be accessed at:
http://canuck.dnr.cornell.edu/HyperNews/get/marked/marked.html

3.2 CHOOSING AN ANALYSIS TECHNIQUE

MARK can undertake a number of different types of analysis depending on the type of data collected. The standard analysis is the Cormack-Jolly-Seber model (CJS model hereafter), based on live animal recaptures in an open population. This is the 'Recaptures only' option in the initial specifications menu of MARK, and considers data from animals marked and released into the population and then re-encountered at a later stage. Other types of data include dead animal recoveries, known fate (e.g. radio-tracking), closed models, robust design and multi-strata models and other special versions of models. These are included in MARK but will not be discussed in this paper (refer to the users' guide, Cooch & White (2001), for more details). The basic CJS model has four main assumptions:

- every animal in the population has the same probability of recapture
- every animal in the population has the same probability of survival
- marks are not lost or missed
- all samples are instantaneous and each release is made immediately after the sample

Using Program MARK, the first two assumptions can be addressed by dividing the population into groups, e.g. males v. females. The first two assumptions then become 'every animal in that group has the same probability of survival and recapture'. For example, adult female and juvenile bats are easier to catch than adult males. Preliminary studies using **minimum number alive** (MNA) methods also suggest that the different social groups of bats have different survival rates (O'Donnell 2000b) so, again, the population can be divided into social groups. The third and fourth assumptions provided few issues for the long-tailed bat dataset as the aluminium identity bands remain on the bats for life and the bat captures sessions are immediate with no bats held over time.

3.3 ORGANISING DATA INTO AN 'INP' FILE

3.3.1 Specifying the encounter history

The format of data required for MARK is the **encounter history**. The encounter history is a series of ones and zeros that show whether or not an animal was trapped or seen during each capture session. The underlying **model** or analysis technique will determine the particular format. The format for a 'recaptures only' CJS model is described here, but other models are illustrated in Cooch & White (2001).

It is easier to initially enter and arrange the data in EXCEL and then save the file as an 'inp' file—the file required by MARK once you have made all the changes. The encounter history for the CJS model consists of a series of 1's denoting capture in a trapping session and 0's when the individual was not caught. Therefore, an individual bat caught in the first year, not in the following three years, again in the fifth year and seventh year but not in the sixth, eighth or ninth year would have an encounter history of:

100010100

The encounter history needs to be in one cell in EXCEL. The **concatenate** function, held in the drop-down function menu of EXCEL, allows you to join up the contents of individual cells. The encounter history can refer to an individual or a number of individuals having the same history. Each line or encounter history should therefore have at least one additional column showing the number of individuals with this encounter history:

100010100 3;

The example above shows that three bats had the same history. This could also be written in the format below if you wanted to keep the information on each individual separate:

100010100 1;
100010100 1;
100010100 1;

To remove an animal from the study, change the sign on the frequency column from positive to negative. The example below indicates that this bat was caught in year 1 and year 3 but was found dead and removed from the study:

101000000 -1;

The encounter history can be annotated using the characters /* */ when you want to identify individuals. In the example below, a band number identifies an individual bat, ie. /*3405*/. MARK knows to ignore any comments within /* */ when analysing encounter histories, so other explanatory comments can be included such as column headings or titles:

/* 3405*/ 100010100

3.3.2 Defining coding for attribute groups

Additional columns after the encounter history can also be used to assign each individual into a particular group; for example, in the long-tailed bats there are three social groups. These groups are known as **attribute** groups. Examples of input data are shown below:

/* 2398*/ 101001001 1 0 0;

/* 3405*/ 100010100 0 1 0;

/* 1654*/ 001001011 0 0 1;

In the above example, Group 1 is indicated by 1 0 0, after the encounter history, group 2 by 0 1 0 and group 3 by 0 0 1. The first bat, number 2398, was therefore caught in the first, third, sixth and ninth year of the study and belongs to group 1. Bat number 3405 was caught in the first, fifth and seventh year of the

study and belongs to group 2. Bat number 1654 was caught in the third, sixth, eighth and ninth year of the study and belongs to group 3. After each encounter history there must be a semi-colon.

3.3.3 Individual covariates

In more advanced analyses, more columns can be added to the dataset for individual covariates such as body condition. Covariates are placed after the attribute groups and tend to be continuous rather than fixed numbers and apply to individuals. The help file in MARK suggests that the covariates should be scaled between 0 and 1 to improve the calculation (Cooch & White 2001).

/*2398*/ 101001001 100 0.5;

/*3405*/ 100010100 010 0.7;

The examples above show covariates for body condition in the last column. This means that you are able to test if survival or recapture is dependent on individual body condition.

3.3.4   Saving as an 'inp' file

Data from the EXCEL spreadsheet needs to be saved as an 'inp' file so it is accessible in the MARK programme. The easiest way to do this is to save as 'NAME OF FILE.INP' (it needs to be in inverted commas) and as type FORMATTED TEXT (SPACE DELIMITED). This just saves the active sheet and can be opened later as a NOTEPAD file. Any changes that are made to this sheet must be done in EXCEL and then saved again as the 'inp' file. There are other ways of doing this, but this method works.

For those readers using the Department of Conservation DME system, an explanation of how to save EXCEL files as non-DME compatible files is held on the Intranet under 'DOC resources, distance sampling, frequently asked questions'. I found it easier to save the file as a formatted text file rather than a tab-delineated file. Once you have transferred the file over to the U drive, change the file extension to .inp so that it will be recognised in MARK. Don't worry if the format of the file is changed when you look at it out of MARK, it is OK once it is being used by MARK.

The long-tailed bat data spanned 9 years and we did several trapping sessions each summer. We amalgamated data from the trapping sessions within each season to simplify the data and gave a one or a zero to indicate whether each bat was caught that year. A copy of the bat files used in this guide are available from mpryde@doc.govt.nz.

3.4   Running MARK

Once the dataset is in the appropriate format, it is ready to be analysed by MARK. Click on the program MARK icon and the homepage will appear. Select FILE then NEW and the screen shown in Fig. 1 will appear.

Working from the top left corner of the screen, first SELECT DATA TYPE, RECAPTURES ONLY is the CJS model we used and is the default option. Under the TITLE FOR THIS SET OF DATA, type in an appropriate name to identify the analysis you are about to undertake, then press the button CLICK TO SELECT FILE. Here you can browse the
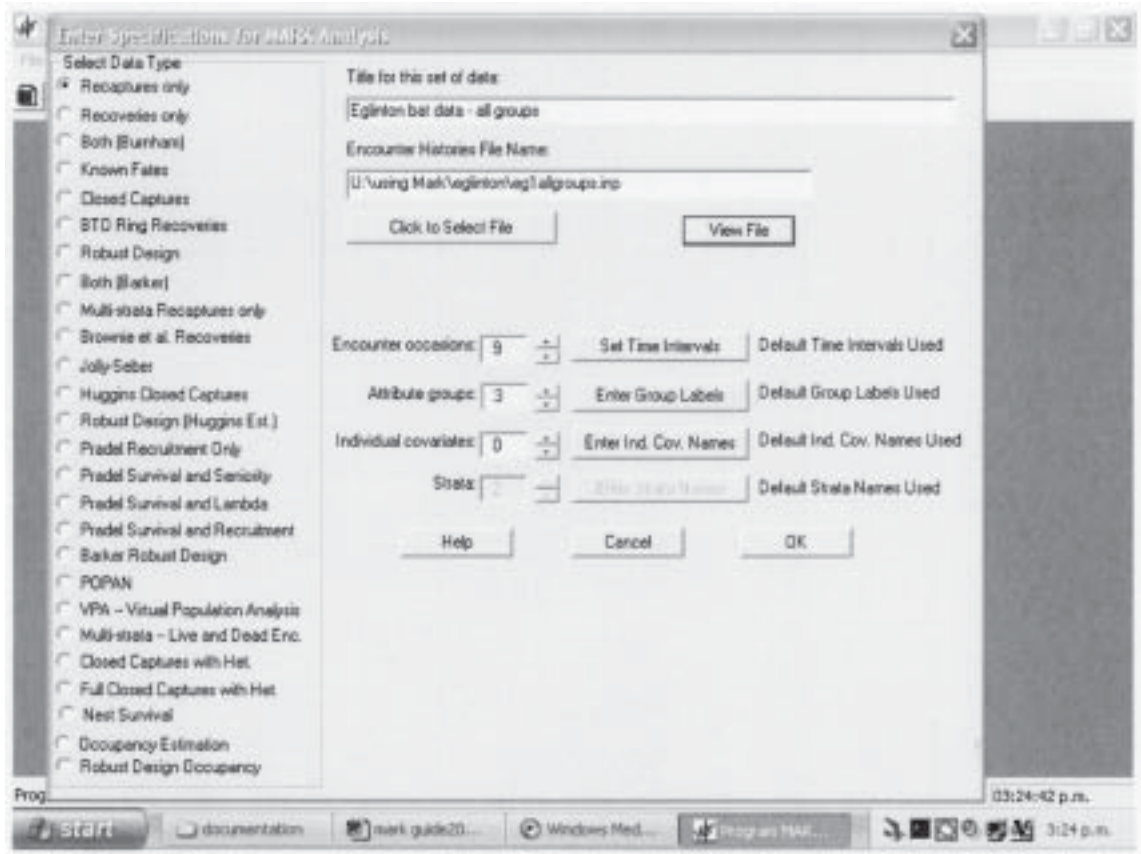
Figure 1.   The NEW opening screen of MARK.

computer's directories and select the 'inp' input file. The pathway will be shown in the ENCOUNTER HISTORIES file name. VIEW FILE allows you to view the file in NOTEPAD where you can check it. ENCOUNTER OCCASIONS refers to the number of times the population is sampled, in our case we had 9 occasions referring to years. The default option for the number of occasions is five, so make sure you change this if your data is different or the program will not run. The time periods will automatically be set to 1 but if you want to change this, then press the SET TIME INTERVALS. In our case we could leave these as 1 since our capture sessions had been amalgamated to one year apart, meaning that MARK produces annual survival probabilities. The ATTRIBUTE GROUPS refers to the number of groups in the data—in this data set there were initially three social groups of bats. We started with the three social groups, ignoring sex and age. These groups can be labelled using the button ENTER GROUP LABELS. The individual covariates button allows you to enter the number of covariate columns—we had none in this example, so we left this field as zero. Once you have filled in all the information, press OK.

A pop-up screen will appear showing that a dbf file has been created. Just press the OK button to proceed. A matrix of the survival of the first group, known as a PIM (Parameter Index Matrix) will appear as shown in Fig. 2.

3.4.1   PIM charts and matrices

The PIM charts and matrices are where the structure of the underlying model can be checked. It is important to understand them because the initial model forms the basis of any other model to be tested. In the screen shown in Fig. 2,
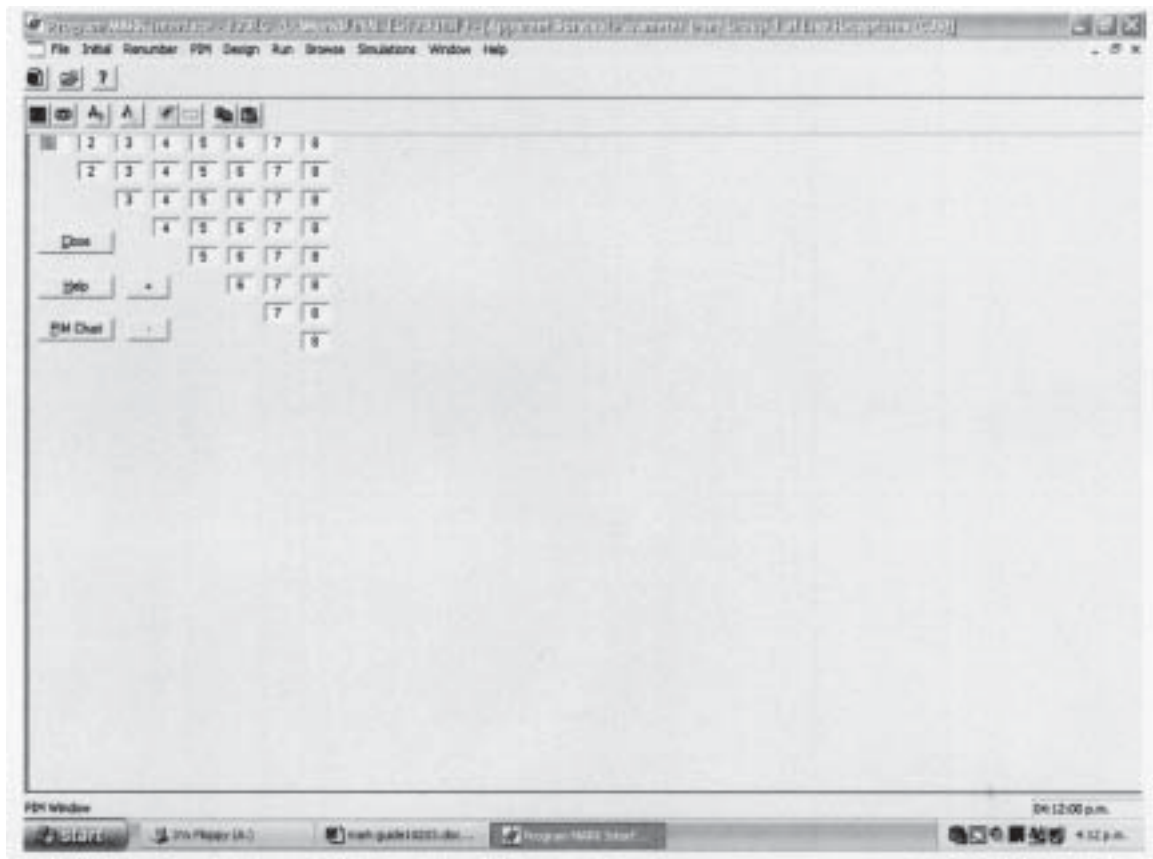
Figure 2. A PIM chart for the survival of bats in Group 1.

only the survival of Group 1 is shown as a matrix, but there are also similar matrices for the survival of the other two groups as well as the recapture estimates of all three groups, giving a total of six matrices (see Fig. 3). Each number on the matrix refers to a survival or recapture parameter. Figure 2 shows that there is a separate parameter estimate for each year for Group 1 bats (1–8). The input data shown in Fig. 1 shows there are 9 occasions when bats were captured but only 8 separate numbers are shown on the PIM. This is explained using the following diagram where, in standard MARK notation, 'ϕ' (phi) is survival and 'p' is recapture.

Years	1	2	3	4	5	6	7	8	9
Survival		ϕ_1	ϕ_2	ϕ_3	ϕ_4	ϕ_5	ϕ_6	ϕ_7	ϕ_8
Recapture	p_1	p_2	p_3	p_4	p_5	p_6	p_7	p_8	

If there are nine years in a study, survival probability refers to the survival between years, so ϕ_1 is survival between years 1 and 2, ϕ_2 is between years 2 and 3, and so on. This means there are only 8 survival parameters. In the same way recapture probability cannot be measured in the first year as there is no comparison with the previous year so, again, there are 8 parameters.

To access the other PIMs, click on PIM in the top row shown in Fig. 2 and select the OPEN PARAMETER MATRIX option. This will produce a list of all the matrices available in the model for your data. Select any or all of these matrices and press OK and the selected matrices will be shown on the screen. To see all the matrices, pull down the WINDOWS menu and select TILE and the screen shown in Fig. 3 will appear. The top three boxes represent survival parameters for each group. Note how the numbers follow on from each other, showing that

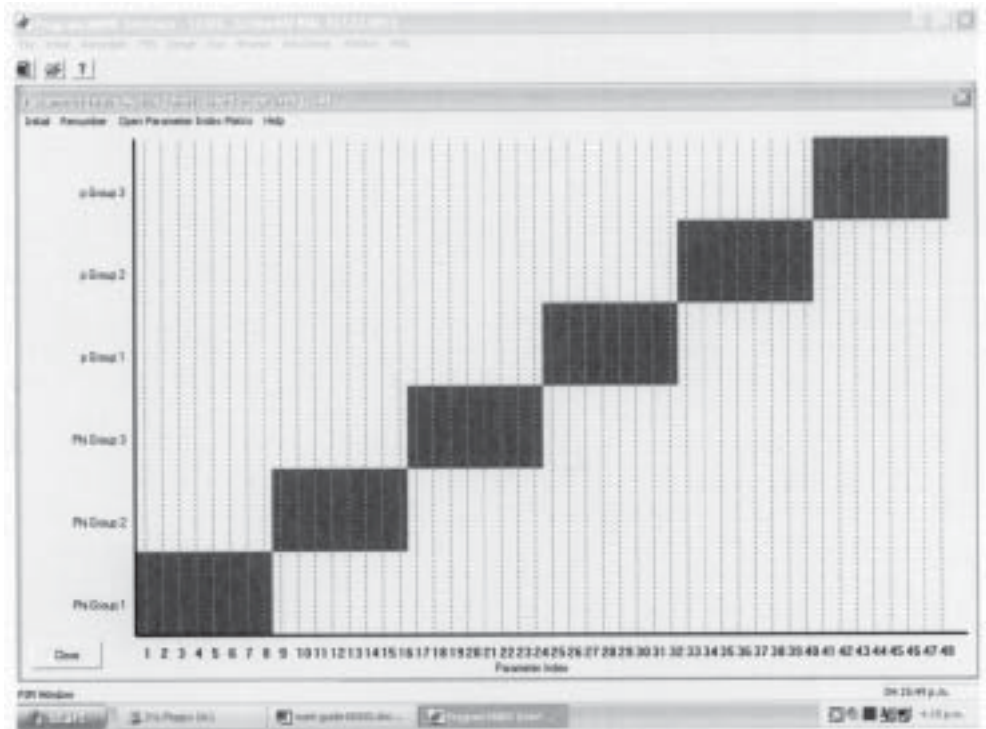Figure 3.   Survival and recapture PIM matrices for all three social groups of bats.

Figure 4.   The PIM chart for survival and recapture probabilities varying with time and social group of bats.

parameters for Group1 are different from those of Groups 2 and 3 and all parameters vary with time (year). The bottom three boxes represent the recapture parameters which, again, vary with time and group.

An easier way of representing the model structure is through the PIM chart. Click on the PIM drop-down menu and select PARAMETER INDEX CHART. A graph will appear, as in Fig. 4.

This graph shows parameter number along the x-axis and attribute group along the y-axis. The numbers from the PIM relate to the numbers along the x-axis. The structure indicates that 24 survival parameters exist in the model (parameters 1–24); that is, 8 estimates for each year of the study for Group 1, 8 estimates for Group 2 (parameters 9–16) and 8 for Group 3 (parameters 17–24). Likewise, there are 24 estimates for recapture probability (p); parameters 25–32 for Group 1, parameters 33–40 for Group 2, and parameters 41–48 for Group 3. To explain this further using examples: parameter 1 is an estimate of survival for Group 1 bats between the first and second year. Parameter 10 is an estimate of survival of Group 2 bats between years 2 and 3, and so on. Parameter 32 is an estimate of the recapture probability of Group 1 bats in the last year of the study.

3.4.2 Running a global model

At this stage the structure of the **global** or **saturated model** has been specified. To run this model, press RUN from the drop-down menu then RUN CURRENT MODEL. The screen shown on Fig. 5 appears. Firstly, give a title for the analysis and for the model name. MARK suggests using the model notation, phi (ø) and p to indicate survival and recapture respectively. On the lower left-hand column of the screen is a list of six LINK FUNCTIONS. The sin link is the default and this is what we used for this analysis—more on this later. The second column is the VARIANCE ESTIMATION that controls how the **variance-covariance** is estimated. This is
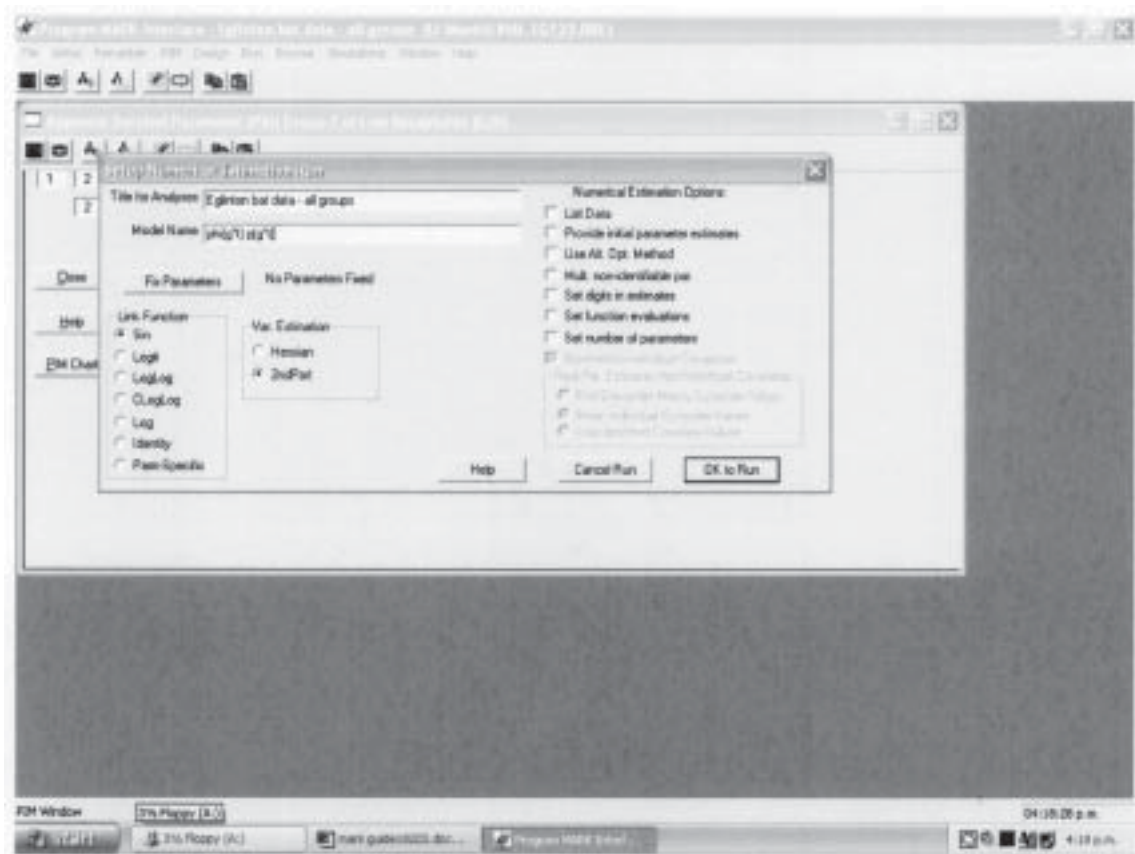

Figure 5. The MARK RUN screen.

important, as it is used to calculate the standard errors of the estimates. The default is 2ND PART and this is what we will use. The button just above the link function allows you to FIX PARAMETERS, which is useful if you want to know whether a parameter can be estimated. In this example it is not necessary (fixing parameters is discussed later in the parameter counting section). The NUMERICAL ESTIMATION OPTIONS on the right side of the screen allows further adjustments to the data and the estimation results. Sometimes adjustments are necessary to get the numerical adjustments to run, but were unnecessary for this example.

Press OK to run and the computer will ask whether you want an identity matrix. Click YES and it will carry on and produce a scrolling DOS window showing the progress of the analysis. A window comes up with some results asking if you wish to append this to the results browser, so click YES if you are happy with the results. This will close the results window and add the result to the browser shown in Fig. 6. The results file is a dbase (DBF) file. In addition to this, CDX and FPT files are created, which are needed to open the DBF file (White & Burnham 1999).

3.5   THE GLOBAL MODEL

The first analysis is the most complicated model, known as the '**global model**'. In this case our global model was that survival (phi or ø) and recapture (p) changes with group (g) and time (t); phi(g*t) p(g*t). It is important to label the

Figure 6.   The MARK results browser showing the results of the model.

models meaningfully, as it is easy to lose track once alternative models have been generated. A global model contains all the variables thought to be important and should be decided at the start of the study. Other models tested will be simplifications of the global model. g*t means a fully interactive model, where there are the main effects, group and time with the * denoting an interaction between the two.

The second column on the results browser, after the name of the model, is the AICc. This is **Akaike's Information Criterion** corrected for small sample sizes (Burnham & Anderson 1998). Correcting for small sample sizes is something MARK does automatically. The Delta AICc is the difference between the model with the lowest AICc and the current model and is used to rank models. The other important columns are the number of parameters and the model deviance. All of these columns are used in model selection and will be discussed further in section 3.8.

At the top of the results browser (Fig. 6) are a number of buttons that can give more details on the results. The parameter estimates for survival and recapture are shown via the fourth button from the left. This brings up a NOTEPAD window that lists 48 parameter estimates of survival and recapture (Table 1). The individual number of each parameter relates to the PIM matrix numbers so you can tell which estimates are for each group of bats. Each parameter has an estimate, a standard error and an upper and lower 95% confidence interval.

These results can be graphed using the GRAPH FACILITY button; the seventh button from the left on the results browser. For the bat example, survival for all three groups can be graphed. A screen with a list of parameters will appear after the graph facility has installed. Highlight parameters 1–8, representing Social Group 1 and press OK—the results for Social Group 1 will be drawn on a graph. On the graph screen press the button ADD SERIES shown on the bottom right-hand corner of Fig. 7 and then highlight the parameters, 9–16 for Social Group 2. This will overlay the results for Social Group 2 onto the graph. This can be done again for Social Group 3 by highlighting the parameters 17–24. The graph is shown below in Fig. 7. I have modified it to a scatter graph using the graph icon in the top left corner and labelled it using the label icon, fifth icon from the right. Further instructions on the graphing option in MARK can be found in the MARK users' guide (Cooch & White 2001).

The graph shows the global model phi(g*T) p(g*t) that has not been corrected for dispersion. Consequently, MARK has problems estimating confidence intervals, especially for social group 2 bats, due to the variance of the data. It is shown here to indicate the graphing capabilities rather than trends in the data. The next section explains how to test the global model and adjust for lack of fit.

TABLE 1. THE FIRST FIVE SURVIVAL PARAMETER ESTIMATES FOR GROUP 1.

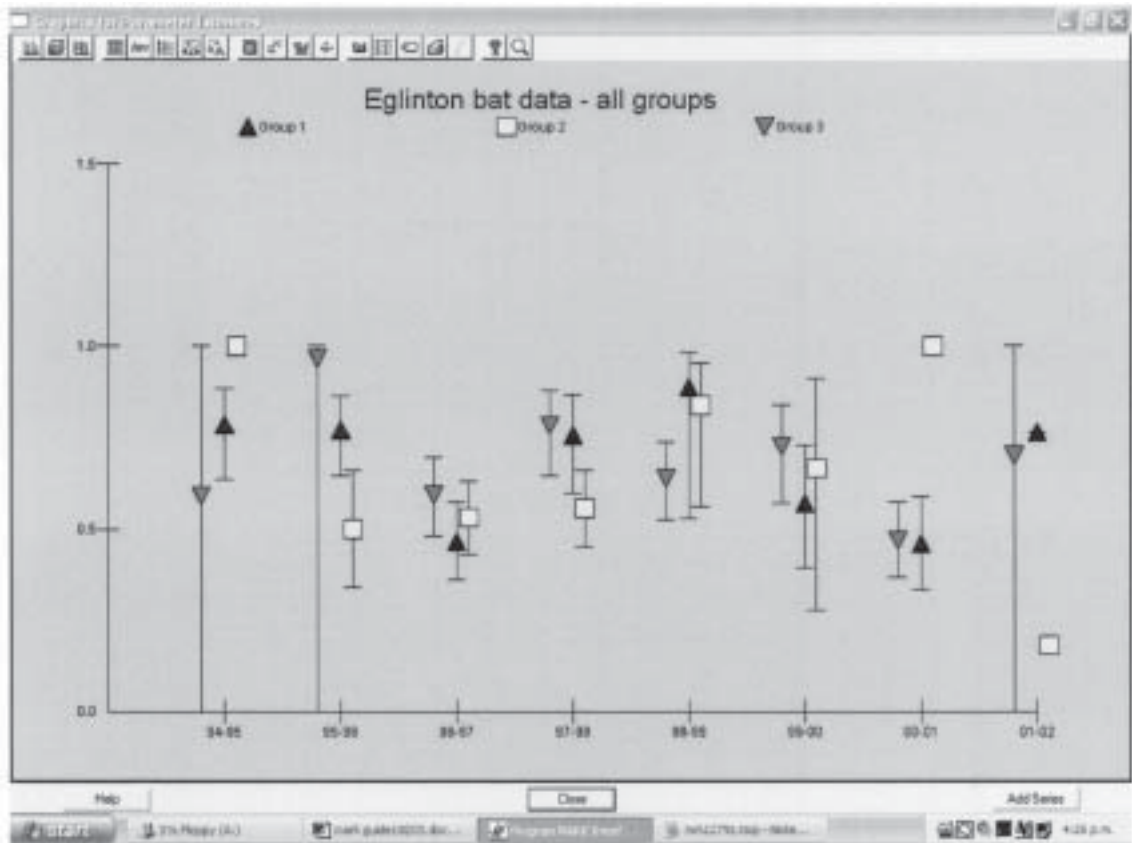| Parameter	Estimate	Standard Error	95% Confidence Interval	
Real function parameters of {phi(g*t) p(g*t)}				
			Lower	Upper
1:Phi	0.7855555	0.0630931	0.6374367	0.8841596
2:Phi	0.7718049	0.0555031	0.6458522	0.8624993
3:Phi	0.4664460	0.0548069	0.3621493	0.5737607
4:Phi	0.7568182	0.0699370	0.5964061	0.8676243
5:Phi	0.8872234	0.0995720	0.5280228	0.9822449

Figure 7. An example of a graph from MARK showing survival rates of bats in the Eglinton Valley from 1994 to 2002. This is the global model phi(g*T) p(g*t) that has not been corrected for dispersion, hence the problems with the confidence intervals, especially in social group 2.

3.6   GOODNESS OF FIT TESTING

We have run one model but now we need to test whether the global model explains the data accurately. To do this we used a **Goodness-of-Fit Test**. This is a simulated boot-strapping procedure that compares the observed data with what the computer would expect if the data conforms to the model. This procedure is held under the TESTS drop-down menu and is called the BOOTSTRAP GOF. You need to test for dispersal or variability of the data. The terms **c-hat** and **deviance** will both measure for dispersion; for example, if the differences between sex and age are unaccounted for then this will result in over-dispersion. If the data are normally distributed, then c-hat will equal one because the average bootstrapped deviance will be the same as the model deviance. You will be asked for the number of simulations (the manual suggests at least 100 simulations and 1000 times for greater accuracy) and the name of the output file, because a new DBF file will be created. Running 1000 simulations will take a while, several hours or even days depending on the complexity of the model.

Once the simulations have finished, the results can be viewed under SIMULATIONS, then VIEW SIMULATION RESULTS, and choose the file that you have just named. Once the file has been chosen, the screen shown in Fig. 8 will appear.

Ordering the results according to the deviance (use the A–Z format button, third to last button from the right-hand side and highlight deviance), makes it easier to scroll down the results looking for the deviance of the original global

Figure 8. An ordered list of bootstrap simulations.

model. If the data follow a normal distribution then the global model deviance will fall somewhere in the middle of the bootstrap distribution. This is unlikely for most ecological data. You can check the number of the bootstrap list using the arrow button (second button from the end) on Fig. 8. If, for example, the model deviance fell between the 987 and 988 out of 1000 simulations, then this means that there is only a 0.012 (1–(988/1000)) chance that the deviance would be that high if the data fitted the assumptions. With the bat data, the model deviance was higher than any of the bootstrap values, meaning a 0.00 probability that the deviance would be so high.

Our data were therefore over-dispersed, meaning we had not included enough explanatory factors in the model, i.e. social grouping and time were not enough to explain the variation in the data.

3.6.1   Adjusting for c-hat

If data are over-dispersed they can be adjusted so that the analysis can continue. This means that the confidence intervals will be large and simpler models will be selected (R. Barker, University of Otago, pers. comm.). To adjust data for over dispersion we calculated the **variance inflation factor** or, to use its more common name, **c-hat**. The default normal distribution for c-hat is 1. There are two ways of calculating c-hat (White & Burnham 1999). The simplest way is to divide the global model deviance from Fig. 6 by the mean deviance of the bootstrap simulations. The button at the right-hand end with the calculator (Fig. 8) gives the mean results of the deviance for the bootstrap simulations. Adjust for c-hat by pressing the ADJUSTMENTS menu and type in the new value. The computer will recalculate the results and give the Quasi AICc adjusted for over-dispersion, instead of AICc.

For the bat data the mean deviance of the bootstrap was 274.41 (this result will vary), whereas the global model deviance was 448.93. This results in a deviance-based c-hat of 448.93/274.41 = 1.64. If c-hat is less than 3, the data are probably OK for using (Lebreton et al. 1992). A large c-hat will mean a more conservative model selection because the AIC will favour models with fewer parameters (Cooch & White 2001).

3.6.2 Examining data further using Program RELEASE

To determine which parts of the dataset are over-dispersed (e.g. data for a certain group or year or certain survival or recapture probabilities), run the program RELEASE held under the TESTS menu as PROGRAM RELEASE GOF. This test runs automatically and comes up with a lot of data. It goes through every data entry and then does three tests. The users' guide talks about these tests in detail (Cooch & White 2001).

Test 1 is useful for looking at the overall difference between groups and to help decide whether or not to pool the data (Burnham et al. 1987). When we ran the bat data through RELEASE, the results for test 1 showed that there was an overall difference in the survival and recapture probabilities between the three groups. A significant result was expected, as we know there is a difference in the social groups (O'Donnell 2000b, 2002).

Test 2 looks at the recapture rates and tests whether the data violate the assumptions of equal recapture rate. The bat data did not fit the model for recapture for all three groups. Test 2 also showed there was insufficient data for all three groups.

Test 3 looks at the survival results and investigates whether the data violate the assumption of equal survival rates. The bat data did not fit the model for survival for Groups 1 and 3.

At this stage I reassessed the data and decided that I had two options: (1) to run the model for just Group 1 (which had the best fit of data) or (2) add sex and age to the population model, combining all three groups in the hope of accounting for the unexplained variance or dispersion.

For the purposes of this guide (to demonstrate 'getting started with MARK', I chose the first option—to continue with the best dataset; that for Social Group 1.

3.7 MODEL BUILDING

I carried on with the analysis, now just using Social Group 1 data and testing for the difference in survival between males and females. I made up a separate 'inp' file for Social Group 1 with the attribute groups as males and females. Over-dispersion for Group 1 was lower (c-hat = 1.44) than for the dataset for all groups combined. Running the data through RELEASE showed variable results for recapture probability but not for survival. As I was interested in survival, this was considered acceptable and I carried on with the analysis.

After adjusting for c-hat I then carried on and ran some more models. There are two ways of building models: manually or by the pre-defined models. The manual method involves changing the models and naming them yourself. This allows you to get to grips with the PIM charts and matrices.

3.7.1   Manually changing models

New models can be created by manipulating the global model. This can be done through the PIM matrices or the chart. The PIM charts for the global model for Social Group 1 data are shown in Fig. 9 where there are nine occasions and two attribute groups—males and females. Therefore 'group' in this case represents sex rather than social group. The left-hand chart in Fig. 9 represents survival parameters for males and the right-hand chart survival parameters for females. The PIM matrices in Fig. 9 show that survival changes with sex and time {phi(g*t)}. Each column represents a different year of the study.

The model shows that survival changes with time and sex because the numbers for each occasion change, i.e. from 1 to 16, and each group has a different set of numbers i.e. 1–8 for males is different from 9–16 for females. If you wanted to change the model and run a model where survival was only dependent on time and not sex, the PIM matrix would change to that shown in Fig. 10.

The model shows that survival changes with time because the numbers change on each occasion from 1 to 8. It also shows that survival does not change with sex, as each set of numbers is the same, i.e. for males and females. You can change the model by changing the numbers in the PIM matrices manually. Alternatively, you can change the PIM chart (shown in Fig. 4) by clicking and

Figure 9. this screen shows how PIM matrices for survival change with sex and time.

Figure 10.   The PIM matrices for survival changing only with time.

dragging the second and third box so that they are stacked on top of the first—this will automatically change the numbers in the PIM matrix. A detailed explanation of how to change the PIM graphs and charts is shown in the MARK users' guide (Cooch & White 2001).

If you wanted to test a model where survival was affected only by sex, and not by time, the PIM matrix would change to that shown in Fig. 11.

Figure 11 shows that survival does not change with time because the numbers on each occasion are the same. However, survival does vary with sex because the number in the group for males is different to that for females.

The PIM charts and the matrices are fundamental to model building within MARK, so it is worth becoming familiar with the process so that you can understand how to change them.

3.7.2   Using the pre-defined models

MARK also has pre-defined models. Click on the RUN menu at the top of the results browser screen and choose the PRE-DEFINED MODELS. This brings up the screen shown in Fig. 12.

This is the same as the RUN screen in Fig. 5, except the FIX PARAMETERS button is now replaced with the SELECT MODELS button. Give a title for your analysis and then press SELECT MODELS to produce the screen shown in Fig. 13.

The survival parameters are shown in the white box and there is a list of four possible combinations. (.) means that survival is constant, i.e. not affected by

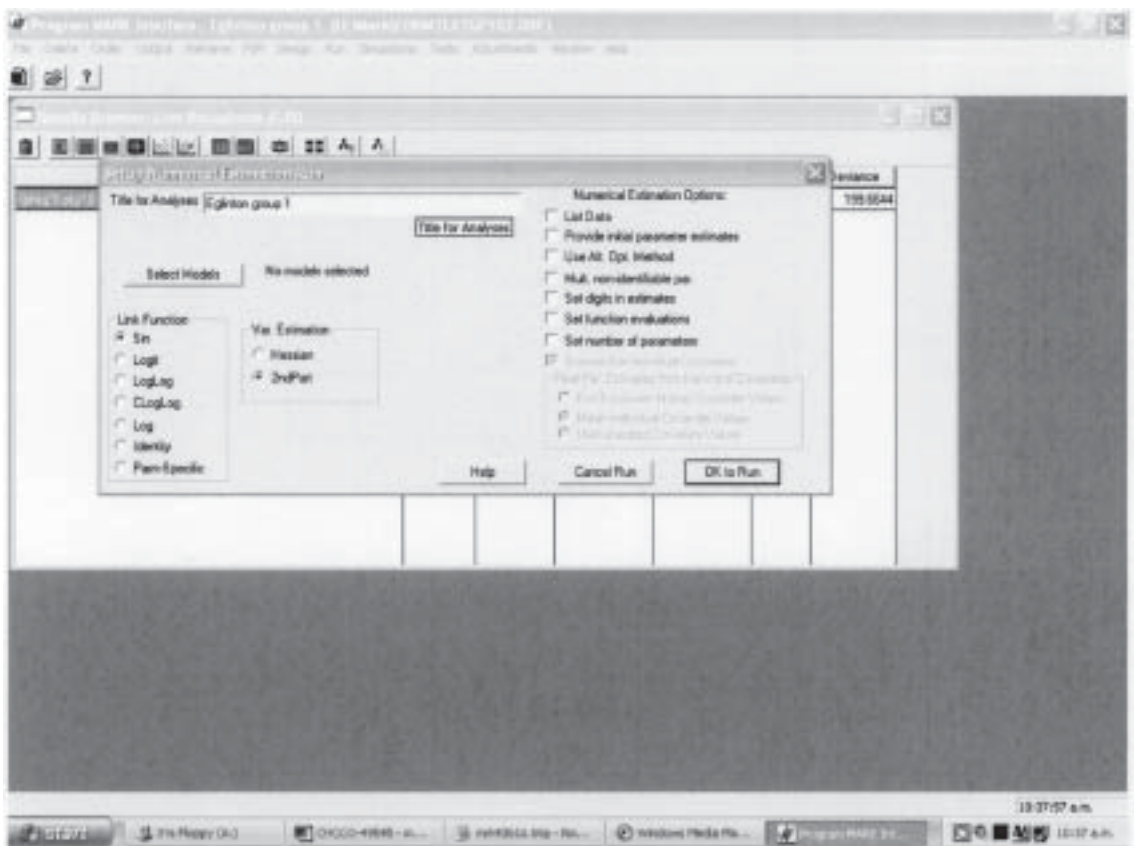Figure 11.   The PIM matrices for survival changing only with sex, and not time.

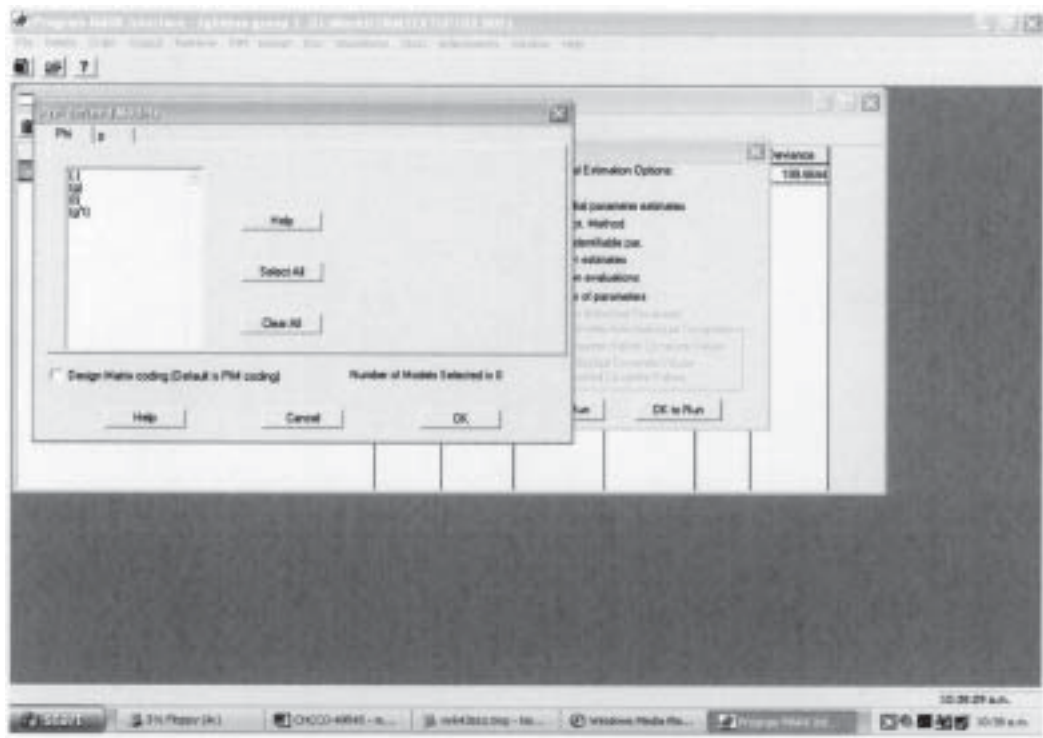Figure 12.   Screen showing the RUN menu for pre-defined models.

Figure 13. Screen showing the list of pre-defined models.

time or group, (g) means that survival varies with group, (t) means that survival varies with time and (g*t) means that survival varies with group interacting with time. If you want to test all possible combinations for group and time, then press SELECT ALL and these four combinations will be highlighted.

If you want to do the same for recapture, press the 'p' tab above the white box and the same list will appear as for survival. Press SELECT ALL again and then OK and the screen will go back to that shown in Fig. 12. Press OK to run and the Results browser screen, shown in Fig. 14, will come up. The program will go through the 16 models selected to be tested and sort them according to the AIC, with the lowest at the top. In this example the **Quasi AICc** (**QAICc**) will be shown instead of the AIC, as the c-hat has already been adjusted for the over-dispersed bat data and the sample sizes are small.

The first model on the list in Fig.14 shows that survival is dependent on time but not sex, and recapture probability is dependent on sex but not time {phi(t) p(g)}. In the second model, survival is again dependent on time and recapture is dependent on the interaction between time and group. The third model shows survival dependent on the interaction between group and time and recapture dependent on group.

Using the pre-defined models is a quick way to get the feel of the data, but if the global model is more complicated, the number of alternative models possible will increase geometrically and it may not be necessary or desirable to run all the possible combinations of models.

Burnham & Anderson (1998) recommend a structured approach to model building where only selected models are run after careful thought has been given to the biology of the species. Lebreton et al. (1992) recommend testing

Figure 14. Screen showing the results browser.

for various hypotheses based on biological questions. They analysed data in two stages, firstly keeping survival the same and changing recapture parameters to find the best recapture model. Secondly, using the model that best described recapture, they kept recapture the same and found the best model for survival. Armstrong & Ewen (2002) and Hoyle et al. (2001) also followed this approach. At the preliminary stage of the bat analysis we ran through the pre-defined models and then designed our own models based on factors for which we had evidence indicating that they were likely to influence survival of the species.

3.8   CHOOSING BETWEEN MODELS

The results browser in Fig. 14 has ordered the results according to the lowest QAICc. The AIC is a combination of the deviance and the number of parameters used to produce a model. The deviance is the difference between the current model and the fully **saturated model** where the number of parameters equals the sample size (White & Burnham 1999). The number of parameters is equivalent to the number of variables used to explain the data. The more parameters, the greater the model flexibility, the better fit to the data and, therefore, the lower the deviance. The cost of the increased number of parameters is reduced **precision** of the estimates and therefore a reduction in what can be inferred from the results (Burnham & Anderson 1998). The AIC measures the cost of the lower deviance against the reduced precision of the estimates. This concept is discussed further in the MARK users' guide and in depth by Burnham & Anderson (1998).

3.8.1 Comparing models using the AIC

The delta QAICc is the difference between the QAICc of the best (lowest value) model compared with other models. If the difference between the model with the lowest QAICc and the alternative model is less than 2, then both models are acceptable. A difference greater than 2 but less than 7 indicates some support for a difference between the models. A difference greater than 7 indicates that the models are different (Cooch & White 2001). Using the results shown in Fig. 11, there is some support for the first model phi(t) p(g*t) being different from the second model because the delta QAICc between this model and the next one is 5.22. The QAICc weightings, which are calculated from the delta QAICc values, show the relative support of the models. In this case the first model phi(t) p(g) has 92% of the weight and the second model phi(t) g(g*t) has 7%. The other models have negligible support. This suggests that from this analysis bat survival is affected by time but there is no difference between males and females, and recapture different for males and females but does not change over time.

3.8.2 Comparing models using LRT

The other method of comparing models is to use the **Likelihood Ratio Test** (LRT). This can only be used for models that are **nested** within the global model (i.e. where a simpler model is created by removing a factor from the other model). For example, phi(t) p(g*t) and phi(g) p(g*t) are nested within phi(g*t) p(g*t). However, phi(g) p(g*t) cannot be compared with phi(g*t) p(t) because neither is nested within the other. The LRT test assesses whether the increase in deviance that occurs when you simplify a model is statistically significant, and therefore whether the more complex model needs to be retained. There is debate on the value of using AIC or LRT tests, reflecting the different philosophies of model selection (Burnham & Anderson 1998). The manual suggests to use the LRT test when the difference in AIC is less than 2 (Cooch & White 2001).

To perform a LRT, click on the TESTS menu and press LR TESTS. This will bring up a list of all the models that have been run. Click on the models you wish to test and press OK. A screen of the results will appear showing the χ^2 and the p value for the test as shown for the bats in Table 2. The difference between the first two models in Fig. 14 is significant ($\chi^2 = 22.598$, p = 0.0468).

Both the AIC and the LRT results provide some support for the first model being the best for explaining survival in long-tailed bats from Social Group 1. The model shows that survival is dependent on time and recapture probability is dependent on sex.

TABLE 2. RESULTS OF A LIKELIHOOD RATIO TEST COMPARING MODELS 1 AND 2 FROM FIG. 14.

REDUCED MODEL	GENERAL MODEL	χ^2	DF	*P*
{Phi(t) p(g)}	{Phi(t) p(g*t)}	22.598	13	0.0468

3.8.3   Model averaging

If two or more models have similar weighting, you may want to do model averaging. Model averaging takes account of the contribution of all the models and produces an average survival and recapture estimate for each occasion. The weighted average includes an estimate and a standard error. Model averaging is useful when there is no obvious best model among a number of good candidate models. The process is further explained in the MARK users' guide (Cooch & White 2001).

3.9   THE DESIGN MATRIX

At this stage the models are fairly simple and it is probably best to keep them that way if you can. However, in our case the analysis involved a comparison of two groups—males and females—where we suspected there was an additive response between groups rather than an interaction. To examine the prediction that male and female bats were affected in the same way by environmental factors such as temperature and predators, we used the design matrix. This is where the analysis gets complicated, so you have been warned! This section on the design matrix is not meant to be comprehensive, it is just to give an idea of what can be done within a design matrix. Reference to the MARK users' guide (Cooch & White 2001) and discussion with other MARK users is recommended.

3.9.1   Additive models

The initial global model (g*t) is a combination of an interactive and an additive response. This can be explained using the equation g*t = g+t+g·t

This means that the global model is a combination of group and time and the interaction of group and time. To test for an additive response where each group is affected in the same way the interaction (g·t) needs to be omitted. This involves a modification of the design matrix. An easy way to test for an additive model is in the pre-defined model section. Click on the DESIGN MATRIX CODING button as shown in Fig. 13 and the g+t model will come up in the white box above and is available for selection. This will allow you to run an additive model without understanding the design matrix. Eventually, if you continue with MARK analysis, you will need to be able to understand and manipulate the design matrix. The MARK users' guide contains a good section on the design matrix so I won't attempt to explain it in this report.

The design matrix looks very complicated and confusing, as it is a huge spreadsheet of ones and zeros, but once you work out the sections it becomes a lot easier to understand. There are three types of design matrices held under the drop-down design menu: full, reduced and identity. I used the full design matrix at first because it was explained in detail in the users' guide (Cooch & White 2001). I moved onto the identity matrix after consulting with other MARK users when my models became more complicated. This is, however, beyond the scope of this report.

The design matrix uses the option of LOGIT on the LINK FUNCTION in the RUN menu as in Fig. 5. The logit function is good for additive models and will automatically be chosen by MARK if you are using the design matrix. The sin link gives an accurate count of parameters, so should be used when the design matrix is not needed (Cooch & White (2001) and section 3.9.3 below).

3.9.2 Covariates

The design matrix also allows you to test for the effects of other variables, such as environmental factors. For example, we tested for the effect of changes in temperature on the survival of long-tailed bats. Environmental factors can be incorporated into the design matrix as covariates. A temperature effect can be thought of as a simplification of time. We used a similar procedure to assess whether year-to-year variation in survival may be due to changes in predator abundance. Again, the MARK users' guide explains this well with examples (Cooch & White 2001).

3.9.3 Counting parameters

This is an important concept to understand once you move onto additive models because the computer sometimes gets the parameter count wrong and you have to know when and how to change it. The parameter count is essential for selecting between models. There is a section on counting parameters in the users' guide that it is advisable to read (Cooch & White 2001). This section is currently being reviewed (Evan Cooch, pers. comm.).

The parameter count is accurate as long as you use the sin link (see Fig. 12). You can use the sin link as long as you don't use the design matrix. You should not use the design matrix unless you are testing for an additive model. Models constructed using the sin link form a basis for checking the parameter count for additive models where the logit function is used.

In the long-tailed bat data for group 1, there are two groups—males and females—and nine encounter occasions. The global model, phi(g*t) p(g*t) will have 32 parameters, made up from 2(groups)*8(time periods) so (2*8)+(2*8) = 32. However, only 30 parameters will be estimable, because the last survival and recapture parameter in each group cannot be individually identified, as there are no more occasions for a comparison. The computer therefore estimates these as a single parameter.

If the parameter count on the results browser is not 30, then you can investigate your data by looking up the OUTPUT menu and choosing INPUT DATA SUMMARY in the results browser (Fig. 14). This gives a summary of the captures and it will be obvious, if there are no captures for one session, why the computer cannot give an estimate or if there are any gaps in the data. Parameters that can be identified may not be estimable due to sparse data. The REAL PARAMETER ESTIMATES (fourth button from left on Fig. 14) allows you to check the value the computer has estimated. Often with problem parameters the standard errors will be high. The logit function gets confused with parameters at the boundary and tends to not estimate them. To see whether the parameter can be estimated, you can fix this parameter (Fig. 5) at a different value and run the model again to see whether the deviance changes. If the deviance changes, the parameter can be estimated, so you can alter the parameter count. This is done using ADJUSTMENTS on the results browser and NO. OF PARAMETERS. Parameter counting is difficult and it is advisable to get further advice if you move onto complicated models.

3.9.4 Results using the design matrix

The long-tailed bat data were analysed using the design matrix to build additive models and to test for the covariates 'predators' and 'temperature'. Figure 15 shows all the models tested and Table 3 highlights the first four.

Figure 15. All the models tested using the design matrix, including examination of the effects of temperature and predators on the survival of long-tailed bats.

The best model chosen was phi(g+pred) p(g+t), i.e. survival changes with group and predator abundance and recapture changes with group and time. This means that the survival of males and females is different but they are affected in the same way by predator abundance. There is support for this model because the delta AIC is greater than 2 and the model weighting is 0.68, showing that the model is supported by 68% of the data. The LRT shows that the difference between models 1 and 2 is significant, $\chi^2 = 11.139$, df = 3, p = 0.011. Predator numbers were high in the years 1996, 2000 and 2001 (Dilks 1999; Dilks et al. 2003). Survival is greater in low predator years than in high predator years for both males and females, as identified by the best model and shown in Table 4.

TABLE 3. THE FIRST FOUR MODELS CHOSEN FOR THE ANALYSIS OF GROUP.

MODEL	QAIC	DELTA AIC	QAIC WEIGHT	NUMBER OF PARAMETER	Q DEVIANCE
Phi(g+pred) p(g+t)	579.26	0	0.68	12	155.08
Phi(g+t)p(g+t)	581.37	2.1	0.24	17	146.58
Phi(t) p(g)	584.02	4.8	0.06	10	164.03
Phi(t) p(g*t)	589.25	9.99	0.005	23	141.43

Phi(g+pred) p(g+t) is the best model because it has a difference in AIC (Akaike's Information Criterion) of greater than 2 compared with other models. The QAIC weighting is 0.68 which shows a lot of support for that model.

TABLE 4.   THE CHANGES IN SURVIVAL RATES FOR HIGH AND LOW PREDATORS.

	LOW PREDATORS	HIGH PREDATORS
Survival of males	0.74 (95% 0.61–0.83)	0.42 (95% 0.28–0.58)
Survival of females	0.81 (95% 0.73–0.87)	0.54 (95% 0.43–0.64)

3.9.5   Further analysis

This analysis has shown that survival of one group of long-tailed bats varies over time and is influenced by predators. Dividing the data into individual groups leads to very small sample sizes, and therefore less inference from the results. Further analysis will be done at the population level by keeping all the groups of bats and accounting for sex and age. Our analysis is ongoing—we have just collected the tenth year of data. It is going to be complicated and could take some time. We will be asking for advice! Happy modelling.

4.   Conclusions

This report provides the reader with basic users' knowledge of Program MARK using a worked example. It should be read in conjunction with the MARK users' guide (Cooch & White 2001). Program MARK is a useful tool with which to measure survival rates in threatened species and the results produced can be used in a population viability analysis. The long-tailed bat data for the Eglinton Valley is a complicated dataset with a number of variables. To run the dataset with all the variables is beyond the scope of the beginning user of MARK. Our approach was to use a simplified dataset to explore MARK and become more competent in its use. This learning process has set the scene for the more complicated analysis now required.

5.   Acknowledgments

6.   References

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Appendix 1

GLOSSARY OF TERMS

A priori Not derived from experience, i.e. Hypothesis derived before data is collected

Akaike's Information Criterion (AIC) Tool for choosing the most parsimonious model.

AICc AIC used in small sample sizes.

Attribute A variable that cannot be measured and must be expressed qualitatively, often termed a categorical or nominal variable (Sokal & Rohlf, 1995).

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)

c-hat Variance inflation factor that is a measure of the amount of dispersion in the data. This can be measured using a goodness-of-fit test.

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).

Cohort A group of individuals from one time period e.g. young produced in a given year

Concatenate To link together a number of terms (Oxford Concise Dictionary 9th ed) in one cell.

Covariate An environmental or biological factor explaining some proportion of variation in the data (Lettink 2003: this volume).

Deviance The difference between the current model and the fully **saturated model** for categorical data (White & Burnham 1999). A fully saturated model is one that explains all the variation by representing the data because the number of parameters equals the sample size.

Encounter history A continuous series of variables, usually ones and zeros, each of which refers to a sampling encounter with a particular individual in a population (Cooch & White 2001).

Global model A model containing all the associated parameters and variables thought to be important. Other models in the candidate set will be simplified cases of the global model. The global model is often the basis for the goodness-of-fit evaluation (Lettink 2003: this volume)

Goodness-of-fit test (GOF) a procedure that tests whether your model adequately fits the data. It tests for over-dispersion which may be caused by lack of independence of animals or other violations of model assumptions. Adjustment for dispersion is by changing the c-hat (modified from Cooch & White 2001).

Likelihood ratio test (LRT) Allows you to test the significance of a particular variable in a model. It measures the difference in deviance between two

nested models and results in a c^2 statistic with n degrees of freedom, where n is the difference in the number of parameters between the two models (modified from Cooch & White 2001).

Minimum number alive (MNA) The minimum number of individuals known to have been alive in the population at the time of the survey, i.e. the number of marked animals encountered during or after that survey (Thompson et al. 1998).

Model A mathematical simplification of reality that represents our understanding of how a system operates (Lettink 2003: this volume).

Nested Models are nested if one model is created by deleting one or more variables from the other model (Cooch & White 2001).

Open population A group of individuals not fixed within a defined area and time period, i.e. there could be births, deaths, immigration and emigration (modified from Thompson et al. 1998).

Parameter An unknown numerical quantity associated with some measure of a target population, e.g. abundance or annual survival (modified from Thompson et al. 1998).

Parsimony The concept that a model should be as simple as possible. The most parsimonious model is that which adequately explains the data with as few parameters as possible (Cooch & White 2001).

Population A group of individuals within a specified area.

Population viability analysis A computer-intensive simulation procedure aimed at predicting population trends for a range of different scenarios (e.g. alternate management regimes, varying levels of predation or harvesting), based on available knowledge of population parameters (e.g. survival rates, recruitment) (Lettink & Armstrong 2003: this volume).

Precision The degree of spread generated from repeated samples (Thompson et al. 1998).

Quasi Akaike's Information Criterion (QAIC) AIC that has been adjusted for over-dispersion.

QAICc AIC that has been adjusted for over-dispersion and small sample size.

Variance A measure of precision in continuous data, where high and low variance indicate poor and good precision respectively (modified from Thompson et al. 1998).