Invertebrates: mark-recapture methods for estimating abundance

Version 1.0

This specification was prepared by Alison Evans in 2016.

Contents

Department of Conservation
Te Papa Atawhai

Synopsis

Mark-recapture methods are used to estimate how many individuals of an animal species are present. The methods are based on the principle that if you sample and mark an unknown proportion of the population, release them and allow them to completely mix with the unmarked individuals and then sample the population once again, you can estimate the total population and how it changes over time (Southwood 1966).

Mark-recapture methods have been used in New Zealand to study bird populations (Scofield et al. 2001; Davidson & Armstrong 2002), lizards (Flannagan 2000; Lettink 2008), bats (Pryde 2003) and freshwater crayfish (Rabeni et al.1997) as well as terrestrial invertebrates (Schops 2000; Jamieson et al. 2000; Leisnham et al. 2003; Joyce et al. 2004; McCartney et al. 2006; Watts et al., 2011). A summary of relevant mark-recapture invertebrate studies is provided in 'Full details of technique and best practice'.

There are several types of mark-recapture studies. The most simple is used to collect basic census information or to estimate the minimum number of individuals alive. More involved mark-recapture studies can be used to model the probability of observing an individual as a function of its survival rate and the probability of observing that individual given that it has survived (White & Burnham 1999; McCarthy 2007). For these types of estimates either closed population models, open populations or robust models (which include elements of analysis from both closed and open models) are used (Lettink & Armstrong 2003).

Closed population studies are usually short term and rely on there being no births, deaths, emigration or immigration within the population. Open population studies are more appropriate for studying population trends over time. A number of computer models have been developed that enable researchers to analyse mark-recapture data and these are based on a set of well-defined assumptions. Program MARK (White & Burnham 1999) is recommended for most invertebrate studies as it allows different population parameters to be tested. This program is available as a free download[1] and is supplied with full supporting documentation, which includes a good introduction to mark recapture as well as full descriptions of the different methods, what can be achieved using them and how to use them.

Mark-recapture studies are useful for estimating the size of populations of invertebrate that are rare, cryptic, or are difficult to monitor due to their preferred habitat type. As with other methods for studying invertebrates there is inherent bias. However, this can be minimised by designing the study carefully and choosing appropriate statistical models to analyse the data.

[1] http://www.phidot.org/software/mark/docs/book/

Assumptions

Closed populations:

- No birth, death, immigration or emigration from the population.
- The probability of capturing a marked invertebrate is the same as capturing an unmarked individual.
- Marking does not affect the behaviour and life expectancy of the animal.
- Marks are not lost.
- Marked animals will mix back with the population when released.

Open populations:

- The probability of capturing a marked invertebrate is the same as capturing an unmarked individual.
- Marking does not affect the behaviour and life expectancy of the animal.
- Marks are not lost.
- Marked animals will mix back with the population when released.

Advantages

- If individuals are not easily monitored (difficult to detect) then this method can be used to assess survival and reproduction rates.
- A good method to measure dispersal or migration (e.g. butterflies).
- Can be used to evaluate impacts of threats on survival, record population trends, assess population viability analyses, set performance targets against which responses to management can be measured, and highlight areas where further research is required (Lettink & Armstrong 2003).

Disadvantages

- Marking invertebrates is often time consuming and difficult to do without harming individuals and it can potentially alter their behaviour.
- Open population studies are time consuming and expensive (they require at least five recapture sessions).
- The researcher needs a basic understanding of the analysis to avoid violating the basic assumptions of mark-recapture studies.
- The study design and data analysis may require specialist help, which can be expensive.
- Requires a collection method that is not lethal and doesn't damage the specimens.
- Collection may need to occur at night or when invertebrates are most active.

- Unsuitable for slow moving or territorial species as they don't mix back throughout the population (Henderson 2003).
- Unsuitable for small, mobile populations as you need to mark a good proportion to do analysis (approximately 20% of population).
- Unsuitable for large populations either because you need to mark approximately 20% of the population (Henderson 2003).
- Open population studies are not suitable for invertebrates with a short lifespan, e.g. Lepidoptera, Diptera, Hymenoptera (Manly & Parr 1968).
- Difficult to get equal 'catchability' if male and females have different behaviour.
- Need to know basic biology, i.e. population trends—whether a population is open or closed (open populations are more difficult to study because of the need to allow for immigration, emigration, death, and birth) (Henderson 2003).
- Marking invertebrates can increase the chances of detection by predators.
- All marks, including leg bands, on juvenile arthropods will be lost when the animal moults.

Suitability for inventory

This method is not suitable for inventory.

Suitability for monitoring

Mark-recapture methods provide information regarding population size. Depending on the particular method chosen, they can also be used to assess population dynamics including dispersal, migration, and recruitment. The method can be costly to implement because it is time consuming and requires specialist statistical help but this can often be justified by the high precision of the population estimates obtained and the quality of the scientific information. There may also be limitations or time delays imposed by the habitat, location or conditions that are required to monitor invertebrates (e.g. the invertebrate being inactive because of unsuitable humidity, temperature, wind speed or light conditions). This method is well suited to monitoring species that are rare and cryptic because the results provide precise estimates (provided observer bias is taken into consideration). Some understanding about the biology of the species (or a closely related species) is necessary to avoid conducting research that violates the assumptions of mark-recapture because without this the results may be inconclusive. It is also recommended that where possible a pilot study is conducted to determine the extent of habitat that the population occupies and to get an initial estimate of population size.

Skills

- Ability to accurately identify the species being studied.

- Have a good understanding of the biology of the species (including whether the species is sexually dimorphic and has behaviour that may influence catchability) and have a basic understanding of the species' phenology.
- Ability to collect, mark and release the species unharmed.
- Ability to identify and traverse the geographical area of the study safely.
- Understand the relevant sampling design issues (particularly the definition of survey area), the assumptions of mark-recapture methods and the options available to improve the accuracy and precision of population estimates.
- Understand program MARK and the consequences that violating the assumptions of the methodology can have on the conclusions of the study.

Resources

- Personnel—ideally at least two people required for safety, marking invertebrates and to record data.
- Notebook and pencil to record date, position and data associated with trapping and marking invertebrates.
- Accurate map of area to identify the geographical boundaries of population.
- Torches and/or headlamps to assist searching in cavities or at night.
- Watch or stopwatch to record time and duration of capture session/s.
- GPS to record position of study site and individual traps.
- Tape measure to record distances between sampling points or traps and to record the size of habitat being sampled.
- Invertebrate marking equipment to mark invertebrates for identification on subsequent sampling occasion/s.
- Equipment to live-trap invertebrates—may include live-pitfall traps, nets, beating trays, quadrats.
- Equipment to mark the study site such as pegs or flagging tape. The study site is marked to be easily located on subsequent sampling trips.
- Thermometer, relative humidity meter, and anemometer to measure environmental conditions at the time of capture session/s.
- Camera to record information on vegetation or habitat type and photos for presentations or reports.

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' (doccm-146272).[2]

Prior to collecting any data, it is important to have a clear understanding of which mark-recapture model is going to be used and the specific data requirements of the software. Mark-recapture studies require staff to be familiar with the assumptions and the potential effects that violating these assumptions will have on the population estimates. Mark-recapture studies also require careful design and it is essential that the correct data is recorded and entered into a spreadsheet in a format suitable for the program being used.

Examples of a data sheet, encounter history and program MARK output that were associated with a study of Mt Augustus snails (see 'Case study B') are available. See:

- 'Augusta mark-recapture data sheet' (doccm-394164)
- 'Encounter history for Mt Augustus snails' (doccm-684491)
- 'Program MARK output for Mt Augustus snails' (doccm-684493)

Data collected at the field site should be entered into an Excel spreadsheet that includes the following subheadings:

- Individual identification number of each invertebrate
- Dates of first capture/marking session
- Dates of subsequent capture sessions
- Notes (e.g. if invertebrate is dead/alive or damaged, feeding, mating or has habitat preferences)

Metadata—initial collection information (first capture session):

- Collector's name and affiliation
- GPS location of site or search area
- Relevant conditions or host plant information
- Trap number/sighting number and GPS position
- Number of individuals marked and details of the marking system used (20% of estimated population required)
- General description of the site including GPS position and photos for future reference
- Number and type of traps or location of visual assessments that have occurred
- Any relevant information regarding conditions (e.g. temperature, wind speed, time)
- Number of individuals collected and successfully marked
- Relevant biological information such as whether the individuals are juvenile or adult, male or female, and whether individuals have been checked for damage
- Details of how and when individuals were released

[2] http://www.doc.govt.nz/Documents/science-and-technical/inventory-monitoring/im-toolbox-standard-inventory-and-monitoring-project-plan.doc

Metadata—subsequent recapture sessions:

- Time interval between recapture sessions
- GPS position of collection trap/sighting and details of mark/number/code
- Number and position of any unmarked individuals collected
- Any information regarding distance from original collection point
- Total number of marked individuals recaptured
- Subsequent collection information (second, third, fourth… capture session)
- Date that the traps were set and collected or when visual assessments were made
- Full name and affiliation of the collectors for each trap/visual assessment
- Any relevant information regarding conditions (e.g. temperature, wind speed, time)
- Any relevant information regarding host plant associations or distances from original capture position

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.

If data storage is designed well at the outset, it will make 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.

Ultimately insects collected for inventory should be deposited in a museum or in the National Arthropod Collection administered by Landcare Research.[3] Institutions should be contacted first to find out their requirements.

[3] http://www.landcareresearch.co.nz/resources/collections/nzac

Analysis, interpretation and reporting

Standardised analysis and interpretation allows comparisons to be made at different sites and at different times. Seek statistical advice from a biometrician or suitably experienced person prior to undertaking any analysis.

Assuming that the study has been appropriately designed and assumptions have not been violated, analysis of the data can be completed using program MARK (White & Burnham 1999).

Mark-recapture studies fall into two main categories:

1. Closed populations (where no birth, death, or movement either into or out of the population has occurred during the study)
2. Open populations (where population parameters change during the study)

Closed population studies

Closed population studies are usually conducted over a short time period and can include one or more recapture sessions. The method was first developed by Petersen in 1896 who used it to estimate the size of plaice populations and then developed further by Lincoln in 1930 who studied waterfowl (Southwood & Henderson 2000).

The assumptions for a **single** recapture study using the Petersen–Lincoln estimator are:

- No birth, death, immigration or emigration
- All individuals have an equal chance of being found or collected
- Marks are not lost

The equation used for a **single** recapture study is as follows:

$$\hat{N} = \frac{n_1 n_2}{m_2}$$

Where:

$\hat{N}$ = estimated population size

n_1 = number of animals caught in first capture session

n_2 = number of animals caught in the second capture session

m_2 = number of animals in both recapture sessions

More precise estimates of population size can be gained using multiple recapture sessions. These allow the assumption that ‘all individuals have an equal chance of being collected’ to be relaxed (as this is often not realistic). Bias can be introduced to population estimates if some individuals are more readily recaptured, e.g. male wētā may be more mobile and therefore more easily sighted during a survey or weevils that have been previously attracted to baited traps might be more likely to be recaptured.

The assumptions for a **multiple** recapture study using the Petersen–Lincoln estimator are:

- No birth, death, immigration or emigration
- Marks are not lost

To analyse data collected from multiple recapture studies the software program MARK (White & Burnham 1999) is recommended. This free software can be downloaded from their website[4] and is well supported with online help. Program MARK allows the user to select models that best fit their data and is based on biologically meaningful variables.

Open populations

The models for open populations allow for changes in population estimates resulting from birth, death, immigration and emigration. Open population studies have a similar set of assumptions to those in closed population studies and rely on estimates of capture and survival probability. Open population studies are usually conducted over a longer period of time than closed population studies (e.g. several years) and usually involve a minimum of three capture sessions (Southwood & Henderson 2000). Firstly, the capture probability needs to be calculated and the population sizes for each successive capture session. Once the capture probability is known, it is necessary to estimate the relative proportions of live animals that are not seen and the number of dead animals (Lettink & Armstrong 2003). The most widely used population estimate for open populations is the Jolly–Seber method, which gives good estimates when 9% or more of the population is sampled (Southwood & Henderson 2000).

The Jolly–Seber equation used to calculate capture probability is:

$$\hat{N}_i = \frac{M_i \, n_i}{r_i}$$

Where:

$\hat{N}_i$ = estimated population on day i

M_i = the estimate of the total number of marked individuals in the population on day i

n_i = the total number of individuals captured on day i

r_i = the total number of marked individuals recaptured on day i

[4] http://www.cnr.colostate.edu/~gwhite/mark/mark.htm

The assumptions for a multiple recapture study using the Bailey's triple catch method or Jolly–Seber model are:

- Marks are not lost
- Marked individuals have the same capture and survival probability
- The capture session is short relative to the intervals between sessions

N.B. The assumptions used with multiple marking capture sessions are often difficult to meet for many invertebrate species because not all marked individuals are likely to make it through to the next capture session (due to their short lifespan). To overcome this bias, Manly & Parr (1968) adapted the Jolly–Seber equation so that each individual has the same chance of capture on the ith occasion.

The Manly & Parr equation (Southwood & Henderson 2000):

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

Where:

$\hat{N}_i$ = estimated population on day i

n_i = the total number captured on session i

p_i = the sampling intensity

Full details for analysing data using the program MARK are provided in a free downloadable manual.[5] For a step-by-step example of a preliminary trial on *Powelliphanta augusta,* see Case study B.

Case study A

Case study A: mark-recapture of Cook Strait giant wētā (*Deinacrida rugosa*) on Matiu/Somes Island

Synopsis

Watts et al. (2011) used mark-recapture to estimate the abundance of Cook Strait giant wētā (*Deinacrida rugosa*) on Matiu/Somes Island. The aim of their study was to compare the abundance estimates from mark-recapture with the results from footprint tracking tunnels to determine if tracking tunnels could be used to estimate the numbers of adult giant wētā present. Wētā were marked with small numbered tags glued to the pronotum, the shield-shaped area behind the head.

[5] http://www.phidot.org/software/mark/docs/book/

Wētā were recaptured by making two independent visual searches each night over 7 nights, individually marking every adult wētā found and noting marked individuals seen again. Recapture rates of wētā using visual searches were low and they concluded this was due to the high mobility of wētā, their unknown response to different weather conditions and differences in behaviour of males and females. The study concluded that using tracking tunnels had advantages over visual searching for this wētā species but that their use needed to be supported by more information on the meteorological factors that affect wētā activity.

Objectives

The key objective of this study was to compare the efficiency of non-invasive tracking tunnels with visual searching for adult Cook Strait giant wētā. Mark-recapture was used to estimate the actual number of adult wētā present.

Sampling design and methods

Once it was established that Cook Strait giant wētā footprints could be distinguished from other wētā species, 71 tracking tunnels were placed adjacent to the main track at six locations around Matiu/Somes Island. A previous trial (Watts et al. 2009) had shown that more wētā occurred at the northern end of the island than at the southern end, so different numbers of wētā occurred at the different locations. A total of 206 wētā were individually marked using numbered tags glued to the pronotum and then released. Two visual assessments of wētā abundance (recapture) adjacent to the tracking tunnels were completed each night using two pairs of searchers over 7 nights. This mark-recapture study conformed to the 'robust' design described by White & Burnham (1999) in that the two independent searches per night allowed a recapture probability to be made. It also met the criteria of a 'closed' population model (which assumed no births, deaths, immigration or emigration from the population during the study) and the data were analysed using the program MARK (White & Burnham 1999). Radio transmitters were also attached to six wētā to determine how far individual wētā moved from the original point of capture.

Figure 1. Cook Strait giant wētā with radio transmitter attached. Photo: Danny Thornburrow, Landcare Research.

Results

Cook Strait giant wētā footprints were found in approximately 29% of the tracking tunnels and more footprints were recorded in tunnels baited with peanut butter. Using either baited or unbaited tracking tunnels was more efficient at detecting wētā than visual searching at night: tracking tunnels are set and closed during the day and they involved less time by personnel.

The results from the visual assessment complemented the results from the tracking tunnels with more wētā being recorded at the northern end of the island. The number of wētā seen did not appear to be related to ambient temperature or relative humidity although there was little variation in these factors over the study period.

Recapture rates of wētā in the mark-recapture study were low and the numbers were not sufficient to allow for differences in heterogeneity in the data or for changes in behaviour resulting from capture to be analysed. However, differences in recapture rates resulting from gender and the night of the survey were able to be incorporated into the model and results supported strong differences. The analysis suggested that the estimated population of wētā was higher than the number that were caught and marked during the visual survey. Data from wētā fitted with transmitters suggested that females moved more than males (averages of 21 m and 9 m per night respectively) and that they took refuge during the day in a variety of habitats. Neither male nor female wētā showed any site fidelity although they could remain within a few metres over several nights before moving on.

Limitations and points to consider

This study provides a number of important insights into how to estimate wētā population density.

Cook Strait giant wētā show no site fidelity in contrast to tree wētā, ground wētā or tusked wētā, which return to the same retreat. As such, they mixed through the population and were therefore suitable subjects for a mark-recapture study.

The recapture rates of marked wētā were low despite a reasonably high number of wētā being marked and there was a high level of variability in the estimates of wētā population size. This highlights the difficulty of retrieving data from a species that is mobile.

The tracking tunnels were shown to be successfully used to estimate wētā population size. However, they can only be used when it is possible to clearly identify the footprints of the species being studied. In this case adult giant wētā were the subjects and their footprints were clearly larger than other wētā present.

Individual wētā cannot be identified from their footprints, which means that it is possible that overestimates of the population could occur if one wētā marks a number of different tunnels or if one wētā marks one tunnel multiple times. Thus the tunnels need to be spaced far enough apart so that wētā do not walk through more than one per night. This required supporting information on wētā movement, which was addressed by attaching radio transmitters to the wētā and locating where they had moved to every day.

The tunnel occupancy is also an index of wētā activity and their use needs to be supported by an understanding of the relationships between wētā activity and abiotic factors such as light intensity, temperature and humidity, which the study only partially addressed. Wētā population assessments using mark-recapture will also be affected by these parameters, but the estimate of absolute abundance can be more definitive.

In conclusion, each study will need to consider the merits of the methodology used and be designed to minimise any potential sources of bias.

References for case study A

Watts, C.; Stringer, I.A.N; Thornburrow, D.; McKenzie, D. 2011: Are footprint tracking tunnels suitable for monitoring giant weta (Orthoptera: Anostostomatidae)? Abundance, distribution and movement in relation to tracking rates. *Journal of Insect Conservation 15(3)*: 433–443*.*

Watts, C.; Stringer, I.; Thornburrow, D.; Sherley, G.; Empson, R. 2009: Morphometric change, distribution, and habitat use of Cook Strait giant weta (*Deinacrida rugosa*: Orthoptera: Anostostomatidae) after translocation to Matiu-Somes Island. *New Zealand Entomologist 32*: 59–66.

White, G.C.; Burnham, K.P. 1999: Program MARK: survival estimation from populations of marked animals. *Bird Study 46* (suppl.): S120–S139.

Case study B

Case study B: mark-recapture of land snails (*Powelliphanta augusta*) following translocation to new habitats on the West Coast of New Zealand

Synopsis

Mark-recapture studies are being used to assess the abundance and survival of snails (*Powelliphanta augusta*) translocated to new habitats following expansion of the Stockton Plateau coal mine. In 2007, several thousand snails were translocated from their original habitat into several new areas containing similar habitat but not occupied by *P. augusta*. The fate of these populations is being monitored to assess whether the snails are able to survive with self-sustaining populations in the new habitats.

Objectives

The objective of the mark-recapture studies is to provide annual survival estimates of the translocated snails and to build long-term population models to detect any changes in population size over time (Weston & Gruner 2009).

Sampling design and methods

A monitoring protocol was developed in collaboration with Proteus Consultancy employing the robust design mark-recapture method. First, two pilot studies were completed to test marking techniques and the suitability of mark-recapture as a monitoring tool (Sharpe 2008). This design incorporates elements of both open and closed populations and involves multiple capture sessions (Lettink & Armstrong 2003). The protocol consists of estimating population size by sampling annually (primary interval; open population aspect) for a 3- to 5-year period with each annual sampling consisting of several independent surveys (secondary interval; the closed population aspect) completed within 2 weeks of each other. The snails are marked individually using numbered polyethylene tags (Hallprint). A separate study to test the reliability of the tags is being conducted by double-tagging individual snails. Monitoring began in 2009 at two permanently marked sites (West 1 and Site A); each site being part of a larger habitat area. Snails were collected by methodically searching for them on warm humid nights by four staff using torches. Marked and unmarked snails were recorded individually on each survey. Unmarked snails were marked and all snails were released after recording the shell size and weight. The data were analysed by Proteus Consultancy, using the Huggins estimator in program MARK (MacKenzie 2009). This allowed four covariates to be incorporated into the analysis: shell size, snail weight, short-term changes in catchability and long-term changes in catchability.

Results

The results given by MacKenzie (2009) showed that from seven repeated searches (the closed population aspect) West 1 had an average population estimate of 103 snails (95% confidence interval 78–167). Site A, from three closed population surveys, had an average population estimate of 347 snails (95% confidence interval 245–546). Subsequent monitoring in 2010 at West 1 allowed comparisons to be made between annual surveys. For this analysis the Pradel robust design analysis was used and abundance estimates were found to be similar between years (MacKenzie 2010).

Limitations and points to consider

Several recommendations were made following data analysis. These included suggestions that population estimates may have been underestimated because only snails > 20 mm were captured and capture probabilities varied over time, suggesting that at least five surveys were required per site to give precise population estimates. There was also evidence of a negative long-term change in catchability between surveys. This implies that snails were less likely to be recaptured if they had been captured in a previous session (MacKenzie 2009). Unfortunately, the data were not collected in accordance with the methodology outlined in the original protocol developed by Proteus Consultancy in that the survey intervals were too close together to consider the surveys independent. This potentially violates the assumption of a closed population study.

References for case study B

Lettink, M.; Armstrong, D.P. 2003: An introduction to using mark-recapture analysis for monitoring threatened species. *Department of Conservation Technical Series 28a*: 5–32.

MacKenzie, D.I. 2009: Report on monitoring trials for *Powelliphanta* ‘Augustus’. Unpublished report prepared for the Department of Conservation, West Coast Conservancy, Greymouth.

MacKenzie, D.I. 2010: Abundance estimation for *Powelliphanta* ‘Augustus’. Unpublished report prepared for the Department of Conservation, West Coast Conservancy, Greymouth.

Sharpe, H. 2008: The snail and the coalmine: using mark-recapture to estimate population size in translocated *Powelliphanta* ‘Augustus’. Unpublished report prepared for Victoria University, Wellington.

Weston, K.; Gruner, I. 2009: Protocol for mark-recapture monitoring of *Powelliphanta augusta.* Unpublished report prepared by the Department of Conservation, West Coast Conservancy, Hokitika. 5 p.

Full details of technique and best practice

A review of relevant invertebrate studies in New Zealand

Schops (2000) used mark-recapture methods to assess the population dynamics of the flightless endangered weevil (*Hadramphus spinipennis*) on Māngere and Rangatira (South East) islands, Chatham Islands. Local weevil population dynamics in one discrete patch of *Aciphylla dieffenbachii* were assessed in detail. Weevils were marked by gluing coloured plastic bee tags (which have individual numbers on them) onto their prothorax, and in addition, enamel paint was placed on the weevil elytra. The mark-recapture study assumed a closed model to estimate population size on each visit to the island and the data were analysed using the program CAPTURE (Otis et al. 1978). An open model was used to estimate survival and birth rates between visits to the island and the data were analysed using the program JOLLY (Pollock et al. 1990). Results showed that weevil numbers increased markedly with significant recruitment between the 1993/94 and 1995/96 summers, but that the population was not able to be sustained by the host plants and the weevil numbers had declined to 0 by 1997. The weevils were loyal to their patch of host plants with 90% of the weevils remaining within 0.6 m of where they were found over a 24-hour period (Schops 2000).

Jamieson et al. (2000) studied the population biology of mountain stone wētā (*Hemideina maori*) that occupy rock tors in alpine and subalpine areas in the South Island. In their study on the Rock and Pillar Range, both adult and juvenile wētā were marked and released under the same rocks from which they were collected. Adults were marked by first lightly sanding the centre of the pronotum with an emery board. Paper tags (each with a unique three-digit number) which had been waterproofed (with previously applied glue) were then glued onto the pronotum of the wētā. A total of 40 adult female and 26 adult males were marked. An additional 30 wētā were marked on an adjacent rock tor to assess the movement of wētā between tor habitats. Wētā survival and movement was monitored for 3 years, thus an ‘open population’ was assumed. Recapture rates were high and the data were analysed using MARK (White & Burnham 1999). Results suggested that females had a higher survival rate than males (but there was high variability associated with the survival estimates). A majority of adult wētā lived for between 2 and 3 years and few wētā moved between rock tors with most remaining loyal to the rock that they were first found beneath. Jamieson et al. (2000) concluded that mark-recapture was a suitable method to use when studying the population dynamics of wētā. The study of mountain stone wētā was extended by Joyce et al. (2004), who assessed survival of wētā using mark-recapture.

Joyce et al. (2004) used mark-recapture to assess the survival of mountain stone wētā (*Hemideina maori*) at low, medium and high altitude on the Rock and Pillar range. They predicted that the wētā survival would be lowest at the low altitude sites where it is at the edge of its range. The wētā were marked (using tags which were glued to the pronotum) and recaptured over three successive summers between the months of November and May (1999–2002). An open population model was used (assuming birth, death, immigration and emigration within the population) although previous studies had shown that there was little movement of wētā between rock tor habitats (Jamieson et al. 2000). The wētā were also measured and sexed on each capture session. The data were analysed using program MARK (White & Burnham 1999). The results indicated that survival was not dependent on altitude and that the females lived longer than the males. The results also supported earlier studies which had found that wētā were larger at higher altitudes (Dowsett 2000; Koning & Jamieson 2001).

McCartney et al. (2006) used a closed population mark-recapture analysis to assess population dynamics of the Raukūmara tusked wētā. The study assessed population density, sex ratio and age structure of the wētā to enable future monitoring of wētā in response to conservation management. A total of 82 adult and 43 juvenile wētā were marked by covering the pronotum with ‘white out’ correction fluid and numbering them with a unique number using a black marker pen. Once released, wētā were recaptured over 5 consecutive nights. A range of closed population models (that allowed for factors such as wētā age, recapture probability and which night the survey occurred) were used to estimate the number of wētā in the study area. On average, the models predicted that there were 142 wētā with 58% of these being juvenile. When the size of the study area was considered, the density of wētā was estimated to be 0.11 wētā/m^2. The authors found that the models used gave ambiguous results and recommended using sampling methods that give absolute estimates of abundance.

Mark-recapture studies have also been used to monitor populations of the giant land snail *Powelliphanta augusta* that were translocated from their original habitat to previously unoccupied translocation sites. The original habitat became part of an open-cast coal mine near Westport. *Powelliphanta augusta* is restricted in its distribution and threatened not only by habitat destruction but also by predation (Sharpe 2008). The aim of the monitoring is to estimate survival of snails in the new habitats and to detect any changes in population size. Details of the mark-recapture methodology used are outlined in 'Case study B'.

Watts et al. (2011) used the mark-recapture method to estimate the abundance of Cook Strait giant wētā on Matiu/Somes Island. The aim of their study was to determine if footprint tracking tunnels could be used as an index of the number of wētā present by comparing the abundance estimates from mark-recapture with the results from adjacent tracking tunnels. Wētā were individually marked using numbered tags that were glued to the pronotum. Wētā were recaptured by repeated visual searching at night. A standard closed population model was assumed and the data were analysed using the program MARK (White & Burnham 1999). Although their results indicated a low recapture rate, there was a direct relationship between the number of wētā present and the number of tracking tunnels tracked. Thus tracking tunnels could potentially be used to estimate the number of wētā present, but the estimate depends on activity and this varies on the as yet unknown response of wētā to different weather conditions and potential differences in behaviour between males and females (see 'Case study A').

Considerations and marking methods for invertebrates

Depending on the aims of the study, marking methods can vary between different groups of invertebrates, from dusting wasps from the same nest with powder, for example, to attaching a unique number to individuals. When choosing a marking method for your study, the following considerations need to be made:

- What population parameters are going to be measured (e.g. survival, longevity, fecundity)?
- Will you need to mark juveniles or just adults?
- How long will the markers need to remain on the invertebrates?
- Is the species of such high conservation value that marking and capture endangers the long-term survival of the population? (It is recommended that for threatened species a pilot study using surrogates is undertaken prior to the study to ensure the marks do not influence the behaviour or life expectancy of threatened species.)

NB: Only unharmed invertebrates should be released and small flying insects should be released close to a refuge (preferably late in the day) to avoid unusual dispersal (Southwood & Henderson 2000).

Marking requirements

The main requirements of a successful marking system for mark-recapture studies are as follows (Southwood & Henderson 2000):

- Marks must not affect survival or compromise reproductive potential.
- Marks must not alter behaviour, e.g. ability to fly, escaping predators, entering burrows.
- Marks should be applied with minimal stress and handling time.
- Marks on juveniles must not affect growth.
- Marks should not make individuals more vulnerable to predation.
- Marks should be durable, well documented and easily interpreted.

Marking methods for invertebrates

Before deciding on which method to use, it is recommended that staff become familiar with the relevant literature which provides details of the methods used in previous mark-recapture studies. This will provide guidance on which methods work successfully and on which invertebrates. The most common methods used to mark invertebrates include:

- Paints—artist's oil paint, model-plane paint, nail polish, fluorescent enamel paint, metallic car paint and Twink (correction fluid)
- Marker pens—permanent markers, correction fluid, glitter pens
- Stains—dyes, inks
- Powders—'day-glo' powder, fluorescent powder, powder/glue composites
- Mutilation—manual scratching of elytra, clipping elytra or thorax, engraving snail shells, removal of tarsi (Ohba et al. 2013)
- Queen honey bee markers—commercially available individually numbered discs
- Microdots—small polymer discs (diameter 0.5 mm) bearing up to 26 characters of information (Whitehead & Peakall 2012)
- Paper markers—using pre-glued/or waterproofed paper markers
- Bird bands—small-sized bird bands on legs of large invertebrates (e.g. wētā)
- Electronic tags—harmonic radar transponders, micro-transmitters
- Enriching a population with stable isotopes, e.g. ^{15}N-potassium nitrate (Hamer et al. 2014).

Deciding on a time frame for the study

Closed population studies are short term and are usually completed within a month. However, this will depend on the longevity of the species of invertebrate you are working with. For example, most moths, butterflies, wasps and flies would have to be recaptured within days of initial release. Longer-lived species such as beetles, wētā or snails could be studied using open population models which span several months or even years. Open population studies require at least 3 periods of sampling (Southwood & Henderson 2000) but more recapture sessions will give the study more statistical power. The normal movement speed of the study organism should be considered when deciding on the time intervals between relocations. Ground beetles can move quickly and far enough (up to 30 m within an hour; Wallin 1991) to make relocation very difficult in dense forest habitats common in New Zealand. For such organisms, relocation every 10–15 minutes is recommended, at least during the initial phase of the study (Lövei et al. 1997). Movement of invertebrates within their habitat (e.g. site fidelity to particular plants or features in their habitat) is an important factor influencing study design and data analysis in mark-recapture studies.

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Appendix A

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

doccm-394164	Augusta mark-recapture data sheet
doccm-684491	Encounter history for Mt Augustus snails
doccm-684493	Program MARK output for Mt Augustus snails
doccm-146272	Standard inventory and monitoring project plan