A Review of Open Capture-Recapture Models for Biologists in Wildlife and Fisheries

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A REVIEW OF OPEN CAPTURE-RECAPTURE MODELS
FOR BIOLOGISTS IN WILDLIFE AND FISHERIES

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Abstract: Recently there has been a lot of research on capture-recapture
sampling models which is of practical significance. The aim of this article
is to review open capture-recapture models in a manner intelligible to wild-
life and fisheries biologists with little training in statistics. The basis
of the review is the Jolly-Seber model which is discussed in detail. A model
allowing age-dependence of survival and capture probabilities for identifiably
age classes is also presented. This is followed by a brief discussion of the
related models for band recovery data. Design considerations are stressed and
a design which attempts to minimize the influence of unequal catchability of
animals on the parameter estimates is presented.

Useful detailed reviews of capture-recapture models are Cormack (1968),
Seber (1973) and two recent papers from a symposium on sampling terrestrial
bird populations (Nichols et al. 1981, Pollock 1981a). Here the aim is to
give a concise review of current models which apply to open \(^{a}\) populations and
then to illustrate them with examples to show their practical importance.
Emphasis is placed on assumptions, robustness of estimates to assumption
failure, and experimental design rather than the statistical technicalities.

\(^{a}\)Here by open we mean additions (births and/or immigrants) into the
population are allowed, as are permanent deletions (deaths and/or
emigrants) from the population.
For data where there are multiple live recaptures the Jolly-Seber model is first discussed (Jolly 1965, Seber 1965). This is followed by a model which allows age-dependence of survival and capture probabilities for identifiable age classes (Pollock 1981b).

Band recovery models (Brownie et al. 1978) which are suitable for use when marked animals are recovered dead are also discussed very briefly. These models have important applications to waterfowl band returns from hunters and also to fish tag returns from sports or commercial fishermen.

Finally some general design guidelines for capture-recapture experiments are given. The use of simulation as an aid to designing sensible experiments is encouraged. A design which attempts to minimize the influence of unequal catchability (heterogeneity and/or trap response) on parameter estimates is discussed (Pollock 1981c). It requires two stages of analysis and incorporates recent closed population models which allow unequal catchability (Otis et al. 1978).

SOME DEFINITIONS

Typically a capture-recapture study is carried out in the following way. The population under study is sampled K times where K is usually more than two. Each time, every unmarked animal caught is uniquely marked; previously marked animals have their captures recorded; and then most or all of the animals are released back into the population. Thus at the end of the study the experimenter has the complete capture history of each animal handled. Batch marks where all animals captured in a particular sample cannot be distinguished are sometimes used but do not provide as much information and should be avoided if practically feasible.
The typical capture-recapture study described then provides two distinct types of information: (i) information from the recovery of marked animals and (ii) information from comparing numbers of marked and unmarked animals captured at each sampling time. Data from (i) can be used to estimate survival rates, whereas data from (i) and (ii) are necessary to estimate population size and birth numbers. Sometimes survival rate estimation is of primary concern and the type (ii) information will not be collected.

Band recovery studies collect type (i) information for survival rate estimation but in this case there is only one recapture as the animal is recovered dead. Typically the animal is recovered by a hunter or fisherman and he returns the band or tag to the appropriate agency.

THE JOLLY-SEBER MODEL

Often the biologist will be interested in a long term capture-recapture study so that open population models are of interest. These models allow estimation of "survival" rates \( \phi_i \), "birth" numbers \( B_i \) and population size \( N_i \) at the different sampling times. It should be emphasized that in capture-recapture studies it is not possible to separate births from immigration or deaths from emigration so that the "survival" and "birth" parameters are perhaps misnamed.

The stochastic model which forms the basis of all capture-recapture models for open populations is the Jolly-Seber model which was independently derived by Jolly (1965) and Seber (1965).

Parameter Estimation

Here an intuitive discussion of parameter estimation is given. Let us suppose to begin with that \( M_i \), the number of marked animals in the population just before the \( i \)th sample, is known for all values \( i = 2, 3, ..., K \). Notice there are no marked animals at the time of the first sample so that \( M_1 = 0 \).
Given various model assumptions which we discuss later an estimator of \( N_i \), the population size at time \( i \), is the Petersen estimator which is based on equating the following sample and population ratios of marked to total animals

\[
\frac{m_i}{n_i} = \frac{M_i}{N_i}
\]

and on rearrangement gives

\[
\hat{N}_i = \frac{n_i M_i}{m_i}
\]

(1)

where \( m_i \) and \( n_i \) are the marked and total numbers of animals captured in the \( i \)th sample respectively.

An estimator of the "survival" rate from sample \( i \) to sample \( (i+1) \) is \( M_{i+1} \), which is the number of marked animals in the population just before the \( (i+1) \)th sample, divided by the total number of marked animals released after sample \( i \), which is \( (M_i - m_i + R_i) \). Note that \( R_i \) is the number of the \( n_i \) animals captured that are released.

\[
\hat{\phi}_i = \frac{M_{i+1}}{(M_i - m_i + R_i)}
\]

(2)

An intuitive estimator of the number of "births" in time interval \( i \) to \( (i+1) \) is

\[
\hat{B}_i = \hat{N}_{i+1} - \hat{\phi}_i (N_i - n_i + R_i).
\]

(3)

This is the estimated difference between the population size at time \( (i+1) \) (which is \( N_{i+1} \)) and the expected number of survivors from time \( i \) to time \( (i+1) \) (which is \( \hat{\phi}_i (N_i - n_i + R_i) \)).
To complete this outline we also need estimators of the $M_i$ parameters because they are unknown in open populations. This can be obtained by equating the two ratios

$$\frac{Z_i}{M_i - m_i} = \frac{r_i}{R_i}$$

which are the recovery rates of two distinct groups of marked animals. $(M_i - m_i)$ are the marked animals not seen at $i$ while $R_i$ are the marked animals seen at $i$ and released again for possible recapture. $Z_i$ and $r_i$ are the members of $(M_i - m_i)$ and $R_i$ which are recaptured at least once. The estimator of $M_i$ is thus

$$\hat{M}_i = m_i + \frac{R_i Z_i}{r_i}$$

and is defined only for $i = 2, \ldots, K-1$. Replacing $M_i$ by $\hat{M}_i$ in (1) means that $\hat{N}_i$ is defined for $i = 2, \ldots, K-1$ and in (2) means $\phi$ is defined for $i = 1, \ldots, K-2$. Also $\hat{B}_i$ in (3) is only defined for $i = 2, \ldots, K-2$.

The approximate standard errors of these estimators are given by Seber (1973;205). Cormack (1964) presents a model for resighting of marked animals without capture. It is actually a special case of the Jolly-Seber model where $\hat{M}_i$ is still given by (4) and $\phi$ the "survival" rate by (2) but it is not possible to estimate population sizes or "birth" numbers.

**Assumptions**

The Jolly-Seber model makes the following assumptions:

1. Every animal in the population (marked or unmarked) has the same probability ($p_i$) of being caught in the $i$th sample ($i = 1, \ldots, K$), given that it is alive and in the population when the sample is taken.
(ii) Every animal in the population (marked or unmarked) has the same probability \( p_i \) of surviving from the \( i \)th to the \((i+1)\)th sample, given that it is alive and in the population immediately after the \( i \)th release \((i = 1, \ldots, K-1)\).

(iii) Marked animals do not lose their marks and all marks are reported on recovery.

The first assumption is often called the Equal Catchability Assumption and it is often suspect in real populations. There are two general types of alternatives:

(i) **Heterogeneity**: The probability of capture in any sample is a property of the animal and may vary over the population. That is, animals may vary in capture probability according to age, sex, social status and many other factors.

(ii) **Trap Response**: The probability of capture in any sample depends on the animal's prior history of capture. That is, animals may become "trap shy" or "trap happy" depending on the type of trapping method used. Either one or both of these alternatives may be acting in a particular animal population.

Carothers (1973) and Gilbert (1973) have used simulation to study the influence of heterogeneity on the Jolly-Seber estimators. Serious negative bias of population size estimators can result but survival estimators, although negatively biased, are much less affected. Trap response can also have a large influence on the Jolly-Seber estimators. If animals are "trap shy" too few recaptures will be made, resulting in over estimation of population size, whereas underestimation will result from "trap happy" animals. Once again survival rate estimators are likely to be less affected. This has design implications which will be considered later.

Heterogeneity of survival probabilities is also possible in natural populations. Cormack (1972) states that this will have little effect on the Jolly-Seber estimators. This is only true if an animal's survival probability is
independent of its capture probability (Pollock and Raveling 1981). We con­sider this problem further when discussing the band recovery models.

If marking decreases the animal's survival rate then very serious bias can occur because the marked population forms the basis of survival estimation and comparison of the marked with the unmarked forms the basis of population size estimation. A negative bias will occur on survival rate estimators while a positive bias will occur on population size estimators. Some methods of marking fish suffer from this problem (Ricker 1958).

Robson (1969) and Pollock (1975) have shown that it is possible to generalize the Jolly-Seber model to allow for a trap response in survival and capture prob­abilities that lasts for a short time (typically one or two sampling periods after initial capture). The estimators still have a similar form to the original Jolly-Seber estimators but because they only use a subset of the marked population the precision is substantially lower.

The third assumption is also very important because if animals lose their marks the number of recaptures will be too low. The result is over estimation of population size and underestimation of survival rates. Seber (1973:93) gives a good review of methods of marking animals, failure of the assumption, and a method to estimate and adjust for tag loss using a double marking scheme. See also Pollock (1981b).

If the biologist believes it is justified there are "births" only or "deaths" only models which are special cases of the Jolly-Seber model (see Seber (1973:217)). As the number of parameters in these models is less the precision of estimators is increased. Jolly (1981) has also given some other models which reduce the number of parameters. He suggests that sometimes it is realistic to assume a constant survival rate and/or a constant capture rate over the whole study. Un­fortunately these models require computer programs which are not generally available at this time.
Example

Here we consider a two year study on the gray squirrel (*Sciurus carolinensis*) carried out in a mature oak woodland at Alice Holt Forest Research Station, Surrey, England. Squirrels were captured at approximately monthly intervals from November 1972 until September 1974. Multiple capture traps baited with grain were located throughout the area on the ground and disguised by leaves. The squirrels were uniquely marked using a toe clipping method.

The basic statistics required for the Jolly-Seber estimates are given in Table 1 and the parameter estimates and approximate standard errors are given in Table 2. Notice that no estimates are given for periods 12-14 because of the small numbers of captures. Notice also that "survival" estimates sometimes are greater than one and I have recorded them as one. Similarly "birth" number estimates can be negative and I have recorded these as zero.

(Tables 1 and 2 to appear here)

This is a very precise study with relatively small standard errors because typically the capture rates are very high and also the survival rates are high which means that once a squirrel is marked it stays in the population a long time and provides information every time it is captured. Notice also that the precision of estimates does vary a lot. This is mainly due to changes in capture probabilities. It should be emphasized, however, that even in studies where the capture probabilities are constant the precision will not be constant and the sampling periods in the middle of the study will have more precise estimates. Notice also that Manly (1971) found using simulation that the estimated standard errors are usually smaller than the actual standard errors especially when the capture probabilities are low.

In terms of validity of the estimates there are many factors to consider. The biologist felt that migration was negligible so that he interpreted survival
and birth estimates as being representative of true survival and birth numbers. There is likely to be heterogeneity of capture probabilities due to age, sex and other factors and also a "trap happy" response of the capture probabilities. Both departures cause underestimation of population size and to a lesser extent underestimation of survival rates.

Young animals should have been joining the catchable population in April and May. This shows up in high estimates of the birth numbers in 1974 but not in 1973. The biologist expected this because 1973 was a very bad year for squirrel reproduction. It is interesting to note that after all the young animals joined the population in May 1974 there was a large drop in the survival estimate and the population size estimate. Unfortunately this occurred right at the end of the study and there were so few captures in September 1974 so that the estimates are very imprecise.

Popan

Computation of the Jolly-Seber estimates and their approximate standard errors is facilitated by the availability of computer programs. Two simple programs are given by Davies (1971) and White (1971). A very powerful flexible program package called POPAN-2 (Arnason and Baniuk 1978) is now available.

The data required for the programs is each individual's complete capture history together with any attribute data such as age or sex. There is a strong data manipulation capability so that for example it is easy to obtain analyses stratified by age or sex or any other coded attribute data.

Popan-2 has the capability of doing the following analyses (i) The Jolly-Seber model (ii) The "Births" only model (iii) The "Deaths" only model and (iv) The Schnabel Model (Schnabel 1938) for a closed population. It also enables one to carry out various tests of fit to models. Popan-2 is primarily
concerned with open population so that it does not have the capability to perform analyses for the unequal catchability models of Otis et al. (1978) which are for closed populations. For those models there is a special computer program called CAPTURE.

One problem with the Jolly-Seber model is the low precision of estimates when the capture probabilities are small. Arnason and Baniuk (1978) emphasize the importance of pooling samples here and Popan-2 makes it straightforward to perform various types of "pooled" analyses which often increase the precision substantially.

Popan-2 also has a powerful simulation capability. This is useful for biologists to assess the influence of assumption failure on their estimates. It can also be used at the design stage to get an idea of the precision of a proposed study.

THE AGE-DEPENDENT MODEL

Description

The Jolly-Seber model makes the assumption that all animals have the same survival rate over any period. Manly and Parr (1968) suggest a model which allows the survival rate to be age-dependent but where it is not necessarily possible to group the animals into identifiable age classes.

For some species of animals there are several clearly identifiable age classes which are likely to have very different survival rates and also possibly different capture rates. Here I discuss a model (Pollock 1981b) which allows for this and it could have important practical applications. Stokes (personal communication) has also worked on a similar model.

We assume for simplicity of illustration that there is one capture period per "year" for K "years". A "year" is used to represent the period of time an animal remains in an age class and will not necessarily represent a calendar year.
There are \((l+1)\) distinguishable age classes of animals ranging from 0 up to \(l\) (or more) years of age and each age class moves forward one class each "year".

We further assume that each age class has a different capture probability in the \(i\)th sample \((p_{i}^{0}, p_{i}^{1}, ..., p_{i}^{l})\) and a different survival probability from the \(i\)th to the \((i+1)\)th sample \((\phi_{i}^{0}, \phi_{i}^{1}, ..., \phi_{i}^{l})\). Also immigration or emigration can occur for each age class of the population, but births can only occur into the young (age 0) group. Thus, when referring to "survival" we really mean those animals which have not died or emigrated. Similarly, when referring to "recruitment", we really mean births and immigration for young animals (age = 0), but only immigration for the older animals (age greater than 0).

The model parameters are the number of animals in the population of each age class at each sampling time \((N_{i}^{0}, N_{i}^{1}, ..., N_{i}^{l})\); the "survival" rate of each age class \((\phi_{i}^{0}, \phi_{i}^{1}, ..., \phi_{i}^{l})\); the "birth" numbers of each age class \((B_{i}^{0}, B_{i}^{1}, ..., B_{i}^{l})\) and the number of marked animals in the population of each age class from 1, 2, ..., \(l+1\) giving parameters \((M_{i}^{1}, M_{i}^{2}, ..., M_{i}^{l+1})\).

The \(M_{i}^{v}\) parameters require further discussion. There are no marked young animals \((M_{i}^{0}) = 0\) because after one "year" they will have moved into the next age class (age = 1). It is necessary to identify marked animals up to age \((l+1)\) \((M_{i}^{l+1})\) to estimate the survival rate of the age \(l\) animals \((\phi_{i}^{l})\) as we shall see in the next section.

**Parameter Estimation**

The statistics used to calculate the parameter estimates are:

- \(m_{i}^{v}\) is the number of marked animals of age \(v\) captured in the \(i\)th sample.
- \(n_{i}^{v}\) is the number of animals of age \(v\) captured in the \(i\)th sample.
- \(R_{i}^{v}\) is the number of animals of age \(v\) released after the \(i\)th sample.
- \(r_{i}^{v}\) is the number of the \(R_{i}^{v}\) which are captured again at least once after the \(i\)th sample.
\( Z_i(v) \) is the number of marked animals of age \( v \) caught before time \( i \), not caught at time \( i \), and caught again later.

\( T_i(v) \) is the number of marked animals of age \( v \) which are caught at time \( i \) or after time \( i \).

Except for some simple extensions the estimators have a simple intuitive structure similar to the Jolly-Seber estimators.

(i) Marked population

\[
\hat{M}_i(v) = m_i(v) + \frac{R_i(v)Z_i(v)}{r_i(v)}
\]

for \( v = 1, 2, \ldots, \ell-1 \)

\[
\hat{M}_i(\ell) + \hat{M}_i(\ell+1) = m_i(\ell) + \frac{R_i(\ell)Z_i(\ell)}{r_i(\ell)}
\]

There is a similar expression for \( \hat{M}_i(\ell+1) \) and the estimators are only defined for \( i = 2, \ldots, K-1 \).

(ii) Total population size

\[
\hat{N}_i(v) = n_i(v)\frac{\hat{M}_i(v)}{m_i(v)}
\]

for \( v = 1, 2, \ldots, \ell-1 \)

\[
\hat{N}_i(\ell) = n_i(\ell)\frac{\hat{M}_i(\ell) + \hat{M}_i(\ell+1)}{m_i(\ell)}
\]

Notice that it is not possible to estimate \( N_i(0) \) because \( M_i(0) = 0 \) and all the above estimators are only defined for \( i = 2, \ldots, K-1 \).
(iii) "Survival" rates

\[ \hat{\phi}_i(v) = \frac{\hat{M}_{i+1}(v+1)}{\hat{M}_i(v) - \hat{m}_i(v) + \hat{R}_i(v)} \quad \text{for } v = 0, 1, \ldots, \ell-1 \]

\[ \hat{\phi}_i(\ell) = \frac{\hat{M}_{i+1}(\ell+1)}{\hat{M}_i(\ell) + \hat{M}_i(\ell+1) - \hat{m}_i(\ell) + \hat{R}_i(\ell)} \]

Notice the need to estimate \( \hat{M}_{i+1}(\ell+1) \) to be able to estimate \( \hat{\phi}_i(\ell) \) as discussed earlier and all estimators are only defined for \( i = 1, \ldots, K-2 \).

Approximate variances and covariances of the estimators are given by Pollock (1981b) and will not be presented here. Note that sometimes resighting of marked animals without capture is used and then survival rates can be estimated but not population sizes.

Example

This example is from a study on Giant Canada Geese (Branta canadensis maxima) carried out by D. G. Raveling. Individually identifiable plastic neck collars were placed on young and adult geese captured on their breeding grounds at Marshy Point Goose Sanctuary on Lake Manitoba in the summers of 1968, 1969, and 1970. Collared birds were resighted in subsequent years on both the breeding and wintering grounds. For more detail on this interesting study see Raveling (1978).

To illustrate the importance of the age-dependent model we use the female resighting data on the breeding grounds. We consider only two age classes, "Young" (age = 0) and "Adults" (age one year or more) because there were not enough "Subadults" (age one year) captured to consider them separately. The female resighting data is given in Table 3.

(Table 3 to appear here)
Obviously, only collared birds can be resighted so that estimation of survival rates is the object. Table 4 presents the necessary statistics and Tables 5 and 6 the appropriate estimators and their standard errors. Note that "survival" here means a bird survived the year and returned to the breeding grounds. In this study we have good precision on our estimates because there is a very high probability (above 90%) of resighting geese which are still alive and present on the breeding grounds.

(Tables 4 - 6 to appear here)

From retrap data of leg banded birds the neck collar loss rate is estimated to be about 0.25 per year (with a large standard error of 0.05). More recent studies have much lower rates (Hinz, Montana Fish and Game, personal communication). Adjusted survival rates are given in Table 6. They are obtained by dividing the unadjusted rate by the probability a goose will still have its collar. (For example 0.57/ (1-0.25) = 0.76.) The standard errors of the adjusted survival rates are also given (Pollock 1981b) and notice that they are larger than for the unadjusted survival rates due to the inprecision of the collar loss estimate. As expected "Young" have significantly lower survival rates than "Adults".

BAND RECOVERY MODELS

Band recovery models can be viewed as a special case of the open capture-recapture models considered here where animals are recaptured dead. Brownie et al. (1978) have written an excellent monograph on these models suitable for biologists. They also provide two computer programs to aid in their analysis. The first ESTIMATE is useful when adults only are banded while the second BROWNIE is useful when different age classes (typically "Young" and "Adults") are banded and may have very different survival and recovery rates. Brownie et al. (1978) emphasize that their models while phrased in the language of
waterfowl banding studies can be very useful to fisheries experiments. See Youngs and Robson (1975) for an example.

The assumptions behind band recovery models are reviewed by Pollock and Raveling (1981). One problem they consider in detail is the influence of possible heterogeneity of survival rates. In band recovery studies an animal's survival rate is likely to be negatively related to its recovery rate which can result in a negative bias or survival rate estimates.

GENERAL DESIGN CONSIDERATIONS

This author believes that the design of capture-recapture studies deserves serious attention from both statisticians and biologists. Methods of avoiding or at least minimizing assumption failure should be considered as well as the question of precision of the estimators. This section will be very brief because many of the ideas discussed have been presented elsewhere in the paper.

The biologist should attempt to use a marking method which is permanent and does not reduce the survival of the animals. Unequal catchability of animals is a problem which can cause large biases especially to population size estimates. Heterogeneity may be reduced by attempting to sample all sections of the population with equal intensity. Also it may be possible to stratify on known sources of heterogeneity such as sex. One possible design is to mark so that animals can be resighted without capture. The design allows only estimation of survival rates (which are not much influenced by heterogeneity) and there is no problem with trap response. High precision often results (Cormack 1964, Pollock 1981b). Another design (Pollock 1981c) which attempts to minimize the influence of unequal catchability is described briefly in the next section.

Very little has been done on sampling intensity and its influence on precision for open populations. Nichols et al. (1981) give some curves relating the
coefficient of variation of estimates to capture probabilities which should prove useful. The examples in this paper should also give biologists a rough idea of precision questions in proposed studies. It should be noted that survival estimates tend to be relatively more precise than population size estimates which are relatively more precise than birth rates. I also strongly recommend biologists consider using the simulation capacity of Popan-2 to help them design their studies. Given a design has been decided upon one method of increasing precision further is to use one of the restricted models with fewer parameters. For example in some studies a "deaths only" model may be biologically realistic.

A ROBUST DESIGN

Recent important research on closed population models which allow heterogeneity and/or trap response of capture probabilities are described in detail by Otis et al. (1978). A practical problem with these models is that often the biologist is interested in long-term studies where an open population model is appropriate. Pollock (1981c) has suggested a design which allows application of both closed and open population models to the data and provides some robustness to unequal catchability in long-term studies.

Consider the following representation of a capture-recapture sampling experiment:

<table>
<thead>
<tr>
<th>Primary Periods</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>...</th>
<th>K</th>
</tr>
</thead>
<tbody>
<tr>
<td>Secondary Periods</td>
<td>1</td>
<td>2</td>
<td>...</td>
<td>ℓ</td>
<td>1</td>
</tr>
</tbody>
</table>

where we have K primary sampling periods (for example years) and within each
one of these we have \( \ell \) secondary sampling periods which are very close to each other in time (for example \( \ell \) consecutive days of trapping).

The biologist is interested in the population size for each of the primary sampling periods \((N_1, N_2, \ldots, N_K)\). He will also be interested in "survival" rates and "birth" numbers between the primary sampling periods \((\phi_1, \phi_2, \ldots, \phi_{K-1} \text{ and } B_1, B_2, \ldots, B_{K-1})\).

Assuming that the population is approximately closed over the secondary sampling periods within a primary period then the following estimation procedure is possible. "Survival" estimation \((\phi_1, \phi_2, \ldots, \phi_{K-1})\) which is not so influenced by unequal catchability would be using the Jolly-Seber model (equation 2) on the data "pooled" within each primary sampling period. (By "pooled" I mean that we just consider if an animal is captured at least once or uncaptured in each primary sampling period). Population size estimation for each primary sampling period \((N_1, N_2, \ldots, N_K)\) would be using the closed population models in program CAPTURE which allow for unequal catchability (Otis et al. 1978). This estimation would be based only on the captures and recaptures within a primary sampling period. "Birth" number \((B_1, B_2, \ldots, B_{K-1})\) estimators will still be based on equation (3) but now using the population size estimators described above.

A small simulation and analysis of an alligator (Alligator mississippiensis) study (Fuller, unpublished thesis, North Carolina State University) supports the robustness of this design. In the alligator study the biologist felt the population size estimates obtained using this method were much more realistic than the Jolly-Seber estimates and much more consistent with results of some other sampling methods.
CONCLUSIONS

With the advent of powerful yet easy to use computer programs (POPAN-2, CAPTURE, BROWNIE) biologists can no longer afford to use old fashioned capture-recapture methods just on the grounds of simplicity. The aim here has been to familiarize biologists with important open population models that are likely to be useful in practice.

It is imperative that biologists take great care in the design of their capture-recapture studies. Model assumptions as well as sampling intensities require careful and informed consideration. Where possible I would advise biologists to obtain expert statistical help for their studies from the design stage onwards.

LITERATURE CITED


Table 1. Capture-recapture statistics for a gray squirrel population, November 1972 - September 1974.

<table>
<thead>
<tr>
<th>Period</th>
<th>n₁</th>
<th>m₁</th>
<th>r₁</th>
<th>r₁</th>
<th>Z₁</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 Nov 1972</td>
<td>46</td>
<td>-</td>
<td>46</td>
<td>43</td>
<td>-</td>
</tr>
<tr>
<td>2 Dec 1972</td>
<td>46</td>
<td>42</td>
<td>46</td>
<td>44</td>
<td>1</td>
</tr>
<tr>
<td>3 Jan 1973</td>
<td>48</td>
<td>42</td>
<td>48</td>
<td>48</td>
<td>3</td>
</tr>
<tr>
<td>4 Feb 1973</td>
<td>46</td>
<td>42</td>
<td>46</td>
<td>45</td>
<td>9</td>
</tr>
<tr>
<td>5 Mar 1973</td>
<td>51</td>
<td>46</td>
<td>50</td>
<td>46</td>
<td>8</td>
</tr>
<tr>
<td>6 April 1973</td>
<td>37</td>
<td>37</td>
<td>37</td>
<td>35</td>
<td>17</td>
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<td>7 May 1973</td>
<td>41</td>
<td>41</td>
<td>41</td>
<td>40</td>
<td>11</td>
</tr>
<tr>
<td>8 May/June 1973</td>
<td>42</td>
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<td>42</td>
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<td>40</td>
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<td>31</td>
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<td>31</td>
<td>26</td>
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<tr>
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<tr>
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<td>9</td>
<td>8</td>
<td>40</td>
</tr>
<tr>
<td>16 Jan 1974</td>
<td>19</td>
<td>17</td>
<td>18</td>
<td>17</td>
<td>31</td>
</tr>
<tr>
<td>17 Feb 1974</td>
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<td>14</td>
<td>19</td>
<td>18</td>
<td>34</td>
</tr>
<tr>
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<td>27</td>
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<td>32</td>
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<tr>
<td>19 April 1974</td>
<td>36</td>
<td>36</td>
<td>36</td>
<td>32</td>
<td>20</td>
</tr>
<tr>
<td>20 May 1974</td>
<td>45</td>
<td>34</td>
<td>44</td>
<td>33</td>
<td>18</td>
</tr>
<tr>
<td>21 July 1974</td>
<td>74</td>
<td>46</td>
<td>73</td>
<td>15</td>
<td>5</td>
</tr>
<tr>
<td>22 Aug 1974</td>
<td>22</td>
<td>20</td>
<td>22</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>23 Sept 1974</td>
<td>3</td>
<td>2</td>
<td>2</td>
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</table>
Table 2. Population estimates (approximate standard errors) for a gray squirrel population, November 1972 - September 1974.

<table>
<thead>
<tr>
<th>Period</th>
<th>Sample Size</th>
<th>$\hat{N}_i$</th>
<th>$\hat{\phi}_i$</th>
<th>$\hat{B}_i$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 Nov 1972</td>
<td>46</td>
<td>-</td>
<td>0.93(0.036)</td>
<td>-</td>
</tr>
<tr>
<td>2 Dec 1972</td>
<td>46</td>
<td>47.1(0.41)</td>
<td>0.95(0.030)</td>
<td>6.3(0.79)</td>
</tr>
<tr>
<td>3 Jan 1973</td>
<td>48</td>
<td>51.4(0.72)</td>
<td>1.00(0.004)</td>
<td>4.4(1.30)</td>
</tr>
<tr>
<td>4 Feb 1973</td>
<td>46</td>
<td>56.1(1.21)</td>
<td>0.99(0.023)</td>
<td>5.1(1.55)</td>
</tr>
<tr>
<td>5 Mar 1973</td>
<td>51</td>
<td>60.6(1.53)</td>
<td>0.93(0.041)</td>
<td>0.0(1.08)</td>
</tr>
<tr>
<td>6 April 1973</td>
<td>37</td>
<td>55.0(1.24)</td>
<td>0.95(0.037)</td>
<td>0.0(0.00)</td>
</tr>
<tr>
<td>7 May 1973</td>
<td>41</td>
<td>52.3(0.60)</td>
<td>1.00(0.029)</td>
<td>4.0(1.24)</td>
</tr>
<tr>
<td>8 May/June 1973</td>
<td>42</td>
<td>56.7(2.08)</td>
<td>0.89(0.052)</td>
<td>3.7(1.48)</td>
</tr>
<tr>
<td>9 June 1973</td>
<td>47</td>
<td>54.7(1.59)</td>
<td>0.92(0.067)</td>
<td>9.0(3.39)</td>
</tr>
<tr>
<td>10 July 1973</td>
<td>31</td>
<td>59.4(4.69)</td>
<td>0.83(0.066)</td>
<td>2.7(7.07)</td>
</tr>
<tr>
<td>11 Aug 1973</td>
<td>8</td>
<td>52.6(6.47)</td>
<td>1.00(0.000)</td>
<td>0.0(6.47)</td>
</tr>
<tr>
<td>12 Sept 1973</td>
<td>2</td>
<td>- (-)</td>
<td>- (-)</td>
<td>- (-)</td>
</tr>
<tr>
<td>13 Oct 1973</td>
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<td>- (-)</td>
<td>- (-)</td>
</tr>
<tr>
<td>14 Nov 1973</td>
<td>4</td>
<td>- (-)</td>
<td>- (-)</td>
<td>- (-)</td>
</tr>
<tr>
<td>15 Dec 1973</td>
<td>9</td>
<td>59.6(9.20)</td>
<td>0.92(0.114)</td>
<td>0.7(6.99)</td>
</tr>
<tr>
<td>16 Jan 1974</td>
<td>19</td>
<td>55.7(4.41)</td>
<td>0.98(0.067)</td>
<td>14.0(8.64)</td>
</tr>
<tr>
<td>17 Feb 1974</td>
<td>19</td>
<td>67.7(8.52)</td>
<td>1.00(0.071)</td>
<td>6.5(10.59)</td>
</tr>
<tr>
<td>18 Mar 1974</td>
<td>27</td>
<td>75.6(8.17)</td>
<td>0.92(0.066)</td>
<td>0.0(6.52)</td>
</tr>
<tr>
<td>19 April 1974</td>
<td>36</td>
<td>58.5(2.14)</td>
<td>0.99(0.071)</td>
<td>18.8(4.34)</td>
</tr>
<tr>
<td>20 May 1974</td>
<td>45</td>
<td>76.7(6.26)</td>
<td>1.00(0.171)</td>
<td>34.8(9.28)</td>
</tr>
<tr>
<td>21 July 1974</td>
<td>74</td>
<td>113.1(19.00)</td>
<td>0.20(0.047)</td>
<td>0.0(2.33)</td>
</tr>
<tr>
<td>22 Aug 1974</td>
<td>22</td>
<td>22.0(-)</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>23 Sept 1974</td>
<td>3</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>
Table 3. Capture history data of female Canada geese first captured as young (adults).

<table>
<thead>
<tr>
<th>Year</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
</tr>
</thead>
<tbody>
<tr>
<td>X_{11} = 67(47)</td>
<td>X_{111} = 34(29)</td>
<td>X_{1111} = 17(18)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>X_{101} = 2(0)</td>
<td>X_{1011} = 1(0)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>X_{1001} = 2(1)</td>
<td>X_{10011} = 3(0)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>X_{011} = 83(31)</td>
<td>X_{0111} = 40(15)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>X_{0101} = 6(2)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>X_{0011} = 60(27)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

In this example, all recaptures are by sighting neck collar numbers and thus there are no "losses on capture." This means X_{11} = R_{11}, etc. To emphasize the notation X_{101} = 2 is the number of birds collared as young in Year 1, not seen in Year 2, and resighted in Year 3.
Table 4. Basic statistics necessary for parameter estimates of female Canada geese data.

<table>
<thead>
<tr>
<th>i</th>
<th>$R_i(0)$</th>
<th>$r_i(0)$</th>
<th>$T_i(1)$</th>
<th>$R_i(1)$</th>
<th>$r_i(1)$</th>
<th>$T_i(2)$</th>
<th>$m_i(1)$</th>
<th>$z_i(1)$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>129</td>
<td>72</td>
<td></td>
<td>67</td>
<td>47</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>190</td>
<td>89</td>
<td>72</td>
<td>168</td>
<td>99</td>
<td>47</td>
<td>114</td>
<td>5</td>
</tr>
<tr>
<td>3</td>
<td>170</td>
<td>60</td>
<td>89</td>
<td>229</td>
<td>118</td>
<td>104</td>
<td>179</td>
<td>14</td>
</tr>
</tbody>
</table>
Table 5. Estimators (standard errors) of the marked population parameters for female Canada geese data.

<table>
<thead>
<tr>
<th>i</th>
<th>$M_1^{(1)} + M_1^{(2)}$</th>
<th>$M_1^{(1)}$</th>
<th>$M_1^{(2)}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>122.48(6.21)</td>
<td>74.11(3.13)</td>
<td>48.37(1.82)</td>
</tr>
<tr>
<td>3</td>
<td>206.17(28.59)</td>
<td>95.07(9.58)</td>
<td>111.10(11.80)</td>
</tr>
</tbody>
</table>
Table 6. Estimators (standard errors) of the survival rates for "young" and "adult" female canada geese data.

<table>
<thead>
<tr>
<th></th>
<th>( \phi_i(0) )</th>
<th>( \phi_i(1) )</th>
<th>( \phi_i(0) )</th>
<th>( \phi_i(1) )</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.57(0.014)</td>
<td>0.72(0.020)</td>
<td>0.76(0.054)</td>
<td>0.96(0.069)</td>
</tr>
<tr>
<td>2</td>
<td>0.50(0.016)</td>
<td>0.63(0.021)</td>
<td>0.67(0.050)</td>
<td>0.84(0.063)</td>
</tr>
</tbody>
</table>

\(^{1}\) Survival rates adjusted for a 25% neck collar loss rate per year. See text for detail.