On the use of capture-recapture methods for studying swans

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Capture-recapture methods are useful in estimating population size, survivorship, and other parameters when some animals alive in a given time period are not detected by the investigator. A large literature exists describing different capture-recapture models, and several user-friendly computer programs have been prepared to assist with the analysis. Investigators who mark swans (or other species) and then recapture or resight them at intervals might find these methods useful. I briefly review requirements and use of the models and computer programs and indicate how to obtain additional information about them.

Capture-recapture methods include a variety of statistical procedures for estimating population size, survival rates, rates of movements and other parameters. They may be appropriate anytime that animals are captured, marked in some way, released, and later recaptured or resighted. They could also be useful when the animals are individually identifiable because of natural variation in bill colour, plumage, or other attributes. Here I provide a brief overview of the methods and suggest that they might be of considerable value to biologists studying swans.

The basic problem which capture-recapture methods address is that animals may be alive but undetected by the investigator. This means, for example, that survival rates estimated simply as the number of animals known to be alive divided by the number marked at some previous time would underestimate true survivorship. Capture-recapture methods attempt to solve this problem by estimating the encounter (or detection) rates and then producing estimates of survivorship, population size or other parameters that take account of detection rates. To estimate the detection rates, they use information from animals that were not seen in some periods but were seen again at a later time. Many different groups of birds may be distinguished, for example first year males, first year females, and so on, and different detection (and survival) rates may be estimated for each group. The basic principle-estimating detection rates with data from birds missed in some periods but seen later - remains the same and lies at the heart of capture-recapture methods.

Definitions and general comments

In capture-recapture methods, "recapture" can be by resighting; the important point is simply that the bird is recorded either as dead or alive during a specific period. Captures and recaptures must be confined to relatively brief periods because the models assume that all births and deaths occur between (not during) these sampling periods. When this assumption is not fully met, a specialist in capture-recapture methods may be able to assess the seriousness of the problem and suggest appropriate solutions.

Many capture-recapture analyses suffer from two problems. First, death, in these analyses is often indistinguishable from emigration. Thus, animals that leave the study area permanently are counted as having died. If an appreciable number do this, then the mortality rate may be seriously overestimated. The second problem, often referred to as heterogeneous resighting rates, is that all individuals (within a given group distinguished in the analysis) are assumed to have the same detection rate during a given observation period. If some individuals are actually more likely than others to be detected in each period, then resighting rates will be over-estimated. This, in turn, leads to underestimating the number of marked birds alive and may lead to a variety of errors in estimating survival rates and population size. Both of these problems - permanent emigration and heterogeneous resighting rates - can often be reduced by distributing the resighting efforts as widely and evenly as possible.

A number of assumptions must be made be-

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Table 1. Example of a "capture history" table showing how data are arranged for analysis using capture-recapture methods

	Period					
Swan	1	2	3	4	5	Comments
1	1	0	0	0	0	Marked in period 1, not seen again
2	0	1	1	0	1	Marked in period 2, seen in years 3 & 5
3	0	0	1	0	1	Marked in period 3, seen in year 5

fore a capture-recapture analysis can properly be undertaken. They are reviewed in the monographs cited below which should be read carefully before a decision is made about whether capture-recapture analyses are appropriate for a particular study.

Overview of a capture-recapture analysis

The first step in carrying out a capture-recapture analysis is to format the capture and resighting data into a table of "capture histories." Each capture period is represented by one column in the table, and the observations for each bird are summarized on one line. The entry for each bird and period is "0" if the bird was not captured or resighted in the period and "1" if it was captured or resighted. With five periods, the first part of a capture history table might appear as in Table 1. Note that the entry for a given bird and period is the same regardless of whether the bird was seen once, or many times, within the period.

Nearly all capture-recapture analyses are carried out using powerful, but easy-to-use, computer programs which offer the user a choice of many different statistical models. By model, we mean a set of assumptions about how recapture (or resighting) and survival probabilities vary in the population. For example, in one population, it might be reasonable to assume that adult males and females had the same resighting rates, but different survival rates. Young birds might be assumed to have survival rates that were different from adults, but young males and young females might be assumed to survive at the same rate. Assumptions may also be made about differences between birds in different geographic areas.

In general, as the number of different groups (defined as birds with different survival or resighting probabilities) increases, statistical power decreases. Thus, investigators want to use a model with the smallest reasonable number of parameters. One of the major advantages of modern capture-recapture models is that they provide easy-to-use, flexible methods for investigating how well each proposed model fits the data. The basic approach is to calculate chi-square goodness-of-fit statistics for each model, and reject models as unrealistic if the chi-square values are too large. Typically, in capture-recapture analyses, much effort is devoted to exploring different models (often more than a dozen candidates) and deciding which one to use. The final choice of a model is usually made on both biological and statistical grounds. Thus, the statistical analysis may show that several models clearly do not fit the data well, but may be unable to distinguish between a few remaining models. The ecologist then usually picks the most biologically realistic model. If more than one model seems equally realistic, then the one with the fewest parameters is usually selected.

Some widely used capture-recapture monographs

Most capture-recapture methods use a very general statistical method known as maximum likelihood estimation. An early formulation of the capture-recapture problem in maximum likelihood terms was provided independently in 1965 by G.M. Jolly and G.A.F. Seber, and their approach is widely referred to as the Jolly-Seber model for capture-recapture data. Since the mid-sixties several investigators have developed a large body of statistical theory and user-friendly computer programs based largely on the original work of Jolly and Seber. A few of the most widely available ones are described below.

1. One study, closed populations

In capture-recapture terminology, "closed populations" refer to populations with no births or deaths or movements into or out of the population, during the period of study. These conditions almost necessitate that the study be conducted during a short period and that the population be isolated or restricted to a relatively small area. When these conditions are met, then much sim-

pler models - or alternatively models which allow more types of variation than "open population" models - can be used.

Closed population models estimate population size, not survivorship (since births and deaths are assumed not to occur). The different models allow capture or resighting rates to change upon first capture, to vary between individuals, or to vary with different time periods. Some combinations of these sources of variation produce models whose parameters cannot be estimated. The models are described by Otis *et al.* (1978) and White *et al.* (1982). The program is called CAPTURE.

2. One study, open populations, single terminal recapture

These programs were developed for banding studies in which most or all recaptures are of birds shot by hunters or found dead (and thus the reference to a single terminal recapture). Survival and recovery rates are permitted to vary with age class and/or calendar year. The models are described by Brownie *et al.* (1985); the programs are called BROWNIE and ESTIMATE.

3. One study, open populations, multiple recaptures

These models permit multiple recaptures or resightings, for example of neck-collared or individually identifiable swans. Survival and recapture/resighting probabilities may vary with time since first capture, age, or calendar year. Methods are also given for combining open and closed models by assuming that within each capture period there are several additional capture occasions during which the closed population assumptions apply. The models are described by Pollock *et al.* 1990. The programs are called JOLLY and JOLLYAGE.

4. Multiple studies, open populations, multiple recaptures

These programs were developed for cases in which one purpose is to estimate a treatment effect. The specific case involved estimating effects of dams on migrating salmon in the Columbia River. The experiment involved releasing some marked fish immediately above a dam and others immediately below the dam such that one group had to pass through the dam while the other did not. Interest thus centered on whether the survival rates of the groups differed, rather than on estimating the rates' absolute values. The models are described in Burnham *et al.* (1987). The program is called RELEASE.

5. More complex cases

Although the models above handle many of the most-commonly encountered cases, investigators often find that their data do not exactly fit any of the models described above. One case of particular interest involves modelling the survival parameters as functions of covariates such as weather conditions, population density, or observer effort. The program, SURGE, described by Clobert, Lebreton & Allainee (1987) is useful for these and other analyses. A very general program, SURVIV, is described by White (1983 and unpub. ms). It requires more statistical background than the other programs, but may be used to explore the performance of nearly any well-defined capture-recapture model.

For more information

The programs can be obtained free-of-charge (but send your own disk) by writing to:

Dr. James D. Nichols, Patuxent Wildlife Research Center, U.S. Fish and Wildlife Service, Laurel, MD 20708 (JOLLY, JOLLYAGE, some versions of SURVIV)
or
Dr. Gary C. White, Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, CO 80523 (most other programs and the manual for program SURVIV).

Dr. White may be able to supply copies of some of the monographs. Alternatively, Otis *et al.* (1978) and Pollock *et al.* (1990) may be obtained from the The Wildlife Society, 5410 Grosvenor Lane, Bethesda, MD, 20814, USA for $4.75 and $4.45 (US dollars) respectively. Burnham *et al.* (1987) may be obtained from the American Fisheries Society, 5410 Grosvenor Lane, Bethesda, MD, 20814, USA. Brownie *et al.* (1985) may be obtained by writing to Publications Unit, U.S. Fish and Wildlife Service, Washington, D.C., 20240, USA.

Obtaining technical assistance

The researchers who developed these models spend a considerable portion of their time helping other biologists analyze their data. It is appropriate to

contact them directly and seek advice if you first do some preliminary work. Read their monographs and format the data into a capture history matrix as explained above and in Table 1. If at all possible, carry out a few preliminary analyses using their programs. If you do these things prior to asking for their help, then you will find them quite willing to correspond with you and answer questions specific to your analysis. Capture-recapture methods thus present an unusual opportunity for swan biologists to work closely with biometricians in joint analyses of large data sets.

Finally, I am currently interested in applying capture-recapture methods to swan data sets, especially in cases where neck-collared birds have been resighted, and would like to correspond with others having similar interests.

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