

Capture-Recapture Models

Using marked animals to study population dynamics

James D. Nichols

Animal ecologists sample the populations they study in a variety of ways. Those who study bird populations in Hawaiian forests may count the number of birds seen and/or heard while walking a transect line or standing at a fixed point in the forest. Those who study red and grey kangaroos in the arid rangelands of central Australia may count animals from a fixed-wing airplane flying along transect lines. The fisheries biologist in the northern Pacific may count the number of halibut caught in a commercial fisheries operation, and the mammalogist in old-field habitat in eastern North America may count the number of meadow voles caught overnight in a grid of small mammal traps.

All these ecologists share a common problem. They have obtained a count statistic (animals seen, heard, or caught), but in most cases it is likely that this statistic is smaller than the actual number of animals present in the sampled area. That is, they have sampled some unknown fraction of the population of interest.

The count statistic by itself is thus of little use to the ecologist, except to provide a minimum bound on population size. We need to know something about the sampling fraction for the count statistic to be useful. If the

Recent flexible software should help new capture-recapture models be rapidly assimilated into ecology

sampling fraction can be estimated, then this estimate can be used in conjunction with the count statistic to estimate population size.

If C_i denotes our count statistic, p_i our sampling fraction, and N_i the true number of animals, and where i specifies a point in space and/or time, then we can write the following simple relationship:

$$C_i = N_i p_i \text{ (equation 1).}$$

If we can figure out some way to estimate the sampling fraction, then we can estimate population size as:

$$\hat{N}_i = C_i / \hat{p}_i \text{ (equation 2),}$$

where hats denote estimators (statistics that are thought to represent or estimate unknown quantities of interest).

Animal ecologists sometimes refer to count statistics obtained under standardized conditions as "indices" of population size. The indices (C_i) are used to compare population size at different points in space and/or time (i). When count statistics are used in this way, there is typically no attempt made to estimate p_i . Instead,

the standardization of counting conditions is assumed to produce sampling fractions that are equal, on average, for the populations being compared.

This assumption, when true, permits reasonable testing and estimation of differences. For example, assume that standardized counts are made of a particular bird population at times t and $t + \Delta$. The rate of population change, defined here as $N_{t+\Delta}/N_t$, can be estimated using $C_{t+\Delta}/C_t$ if $p_t = p_{t+\Delta}$. However, even in this favorable situation of equal sampling fractions, the variation associated with the sampling process causes $C_{t+\Delta}/C_t$ to yield an estimate of population change that exhibits some bias (Barker and Sauer in press).

The success of this kind of standardization depends on our ability to identify all the factors that influence the sampling fraction and to exert some control over these factors. Unfortunately, sampling fractions frequently vary over time and space in response to factors over which we have no control. For example, when we sample more frequently than once per year, we cannot standardize such factors as weather conditions and behavior of individuals relative to the annual reproductive cycle. The sources of variation in p that we cannot identify are probably more important than those that we recognize but cannot control. Thus, the reasonable use of count statistics as population indices requires an assumption that should be tested and that is frequently false.

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Knowledge of p is also important if we are interested in quantities other than population size. For example, assume that we are interested in survival rate. We might study this rate by releasing a number of marked animals at the beginning of some interval of interest. We could then sample the population at the end of the interval and obtain a count statistic for the number of marked animals still in the population. Once again, however, we would need to estimate the sampling fraction to translate this count into an estimate of the true number of marked survivors. The estimation of p thus becomes the central methodological problem associated with the study of natural animal populations.

Capture-recapture models were developed for field studies in which the count statistics are numbers of marked and unmarked animals caught or, in some circumstances, sighted. These models provide reasonable ways of estimating p (capture or sighting probability in this case) and quantities of biological interest such as population size and survival rate. In this article, I briefly review capture-recapture models, emphasizing important recent advances. These advances permit rigorous tests of a variety of interesting hypotheses about how animal populations work.

The Lincoln-Petersen estimator

The earliest method of estimating population size from marked animals is the Lincoln-Petersen method. The method appears to have been independently discovered a number of times, for example by C. G. J. Petersen in 1889 working in Denmark on the fish called plaice, by F. C. Lincoln in 1930 working on North American waterfowl, by C. H. N. Jackson in 1933 working on tsetse flies in Tanganyika Territory, and even by P. S. Laplace in 1783, who used the basic method with a French birth register and census data from several parishes to estimate the size of the human population of France (see reviews in Pollock 1991, Seber 1982).

The method involves catching an initial sample of n_1 animals, applying marks to each animal, and then releasing the animals back into the pop-



This adult male canvas back, *Aythya valisineria*, was tagged with a nasal saddle in a field study. Photo: G. M. Haramis.

ulation. We then catch another sample of n_2 animals from the population (e.g., we might take this sample the day after the initial sample), and we record the number of animals in this second sample that are marked, denoted m_2 . If N denotes the actual number of animals in the sampled area, then we can write the sampling fraction for the initial sample as n_1/N . If certain assumptions hold true, then the proportion of marked animals in the second sample should estimate the proportion of marked animals in the population, that is,

$$m_2/n_2 = n_1/N \text{ (equation 3).}$$

We can then rearrange equation 3 to obtain the Lincoln-Petersen estimator for population size,

$$\hat{N} = n_1 n_2 / m_2 \text{ (equation 4).}$$

Notice that this estimator (\hat{N}) is of the same form as our general expression (equation 2). We are simply estimating population size by taking a count statistic, n_1 in this case, and dividing it by an estimate of the associated sampling fraction, m_2/n_2 .

The early animal ecologists Petersen, Lincoln, and Jackson appear to have derived the estimator in equation 4 intuitively. Subsequently, biostatisticians derived the estimator using hypergeometric and binomial models. These derivations have led to the development of variance estimators and to slightly modified versions of equation 4 that show reduced bias,

especially when sample sizes are small (see Seber 1982).

Beyond Lincoln-Petersen

The Lincoln-Petersen estimator became an important component of the animal ecologist's methodological repertoire and has seen much use over the years. However, ecologists recognized the need for estimators to handle different sampling situations, and this recognition led to the development of different classes of capture-recapture models. Most of these subsequent capture-recapture models were developed to handle more than two sampling occasions. In these multiperiod studies, animals caught in the initial sampling period are marked individually and then released. In subsequent samples, marked animals that are recaptured are recorded and then released, and unmarked animals are marked and released.

The data resulting from such studies are generally summarized in the form of capture histories. A capture history is simply a row of 1s and 0s, where 1 denotes capture and 0 denotes no capture. The first number in the row corresponds to the first sampling period, the second number to the second sampling period, and so on. For example, consider the capture history 10110. The animal to which this history applies was captured in period one, was not captured in period two, and was recaptured in peri-

Table 1. Possible observed capture histories and associated probabilities in a three-sample study of a closed population under model M_t .

Capture history	Probability
111	$p_1 p_2 p_3$
110	$p_1 p_2 (1 - p_3)$
101	$p_1 (1 - p_2) p_3$
100	$p_1 (1 - p_2) (1 - p_3)$
011	$(1 - p_1) p_2 p_3$
010	$(1 - p_1) p_2 (1 - p_3)$
001	$(1 - p_1) (1 - p_2) p_3$

ods three and four but not in period five. A capture-recapture study yields a capture history for every animal caught. The capture-recapture statistician develops a probabilistic model describing the sequence of events producing each capture history and then derives estimators for quantities of interest from this model.

The kinds of parameters needed to model capture history data differ between model classes that are defined by the idea of population closure. An open population is defined as one that animals can enter and leave (via birth, death, immigration, and emigration) between sampling periods. A closed population is one that does not change composition during the course of the study (i.e., exactly the same animals are in the population and exposed to capture efforts every sampling period).

Capture-recapture models developed for closed populations are typically applied to data collected over a short period of time. For example, a small-mammal trapping grid might be run for five consecutive days, and the resulting data would typically be used in conjunction with closed population models. The Lincoln-Petersen estimator is generally considered in a closed population framework, although the closure assumption can be partially relaxed (Seber 1982).

Open population models are used for long-term capture-recapture studies. For example, a small mammal population might be sampled every four to six weeks or a migratory bird population every year.

Closed population models. Capture histories resulting from studies of closed populations are modeled in terms of capture probabilities. Let p_{ij} denote the probability that animal j from the studied population is cap-

tured in sampling period i . Different models have been developed to incorporate different sets of assumptions about sources of variation in these capture probabilities. The simplest model (called M_0 in the notation of Otis et al. 1978, White et al. 1982) for closed populations assumes a constant capture probability that applies to all individuals over all sampling periods, that is, that $p_{ij} = p$ for all animals (j) and sampling periods (i).

Model M_t assumes that capture probabilities vary among sampling periods but that within a sampling period all individuals exhibit the same capture probability ($p_{ij} = p_i$ for all j). The probabilities associated with each observed capture history in a three-period study are presented for M_t in Table 1. Consider capture history 101 as an example. The probability of being caught in period one is given by p_1 , the probability of not being caught in period two is given by the complement of p_2 (i.e., $1 - p_2$), and the probability of being caught in period three is given by p_3 . The probability of exhibiting capture history 101 is thus given by the product of the probabilities associated with these three events.

Each animal in the population must exhibit one of the capture histories in Table 1 or the unobserved history 000. If we are able to assume that capture fates of individual animals are independent, then the observed numbers of animals exhibiting the different histories follow a multinomial distribution.

A behavioral response to initial capture (trap-happiness or trap-

shyness) is considered in model M_b , where animals that have never been captured exhibit one capture probability and animals that have been captured at least once exhibit a different capture probability. Model M_b considers heterogeneity among individuals in capture probability, such that each individual in the population may have a different capture probability ($p_{ij} = p_j$ for all i). However, neither M_b nor M_t permits variation in capture probability among sampling periods.

In addition to these models permitting single sources of variation in capture probability (time, behavioral response, and heterogeneity), it is possible to consider combination models that incorporate more than one source (i.e., M_{bb} , M_{tb} , M_{tb} , or M_{tbb}). Some of these combination models are so general, and thus have so many parameters, that estimation of population size is difficult. In particular, combination models that include time present problems, as it is difficult to distinguish temporal from other sources of variation.

A comprehensive computer program, CAPTURE, was developed to provide estimates of population size under the models for which estimation is possible (Otis et al. 1978, White et al. 1982). The program also computes goodness-of-fit statistics and between-model test statistics that are useful in testing model assumptions. These tests permit inferences about what sources of variation in capture probabilities are important for a given data set. Test results are also used in an objective model selection procedure. CAPTURE has seen

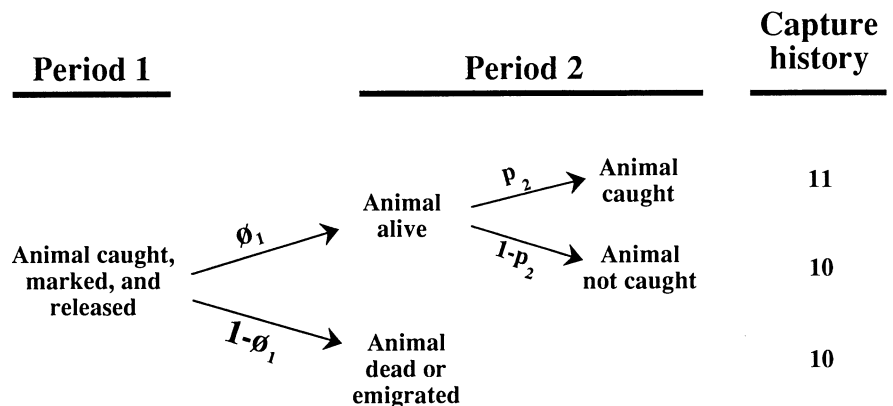


Figure 1. Diagram of events and associated probabilities for an animal released in period one of a two-period study under the Cormack and Jolly-Seber models for open populations.

wide use by animal ecologists over the past dozen years. There has been additional work on models and estimators for closed-population studies over this period (e.g., Chao 1987, Pollock 1991, Pollock and Otto 1983, Pollock et al. 1984, Rexstad and Burnham 1991, and Seber 1986), and an updated version of CAPTURE with some new point and interval estimators is now available (Rexstad and Burnham 1991).

There has also been some interesting recent work on continuous-time models for closed populations (Becker 1984, Wilson in press). Continuous-time models pertain to field situations in which traps are continuously monitored such that animals are processed and released immediately after capture. Capture occasions are instantaneous, rather than occurring over a finite time interval such as a day or an evening, and the exact times (and thus the order) of individual captures are important.

Open population models. Capture histories resulting from studies of open populations are modeled using two kinds of parameters: capture probabilities and survival probabilities. The first of the modern models for open populations were developed independently by Cormack (1964) and by Jolly (1965) and Seber (1965; Brownie (1987) provides a discussion of the distinction between the Cormack and the Jolly-Seber models). Both the Cormack and the Jolly-Seber models permit capture and survival probabilities to vary among sampling periods. Let p_i denote the probability that an animal in the sampled population at period i is captured during that period. Let ϕ_i denote the probability that an animal in the population at period i is alive and still in the population (i.e., has not permanently emigrated) at period $i+1$. Figure 1 is a tree diagram showing the possible events for an animal marked and released in period one of a two-period study, and Table 2 shows the possible capture histories and associated probabilities for animals released in period one of a three-period study.

Both Figure 1 and Table 2 are based on the Cormack and Jolly-Seber models and hence allow for temporal variation in capture and

survival probabilities. As an example, consider the capture history 101 in Table 2. Because the table considers only animals marked and released in period one, we are concerned only with modeling events occurring after period one. The animal must have survived to period two (we know this because it was later caught in period three) and this event (survival) occurs with probability ϕ_1 . The animal was not caught in period two, and the probability associated with this event is $1 - p_2$. Finally, the animal survived until period three (ϕ_2) and was captured at that time (p_3). The probability associated with capture history 101 is thus $\phi_1(1 - p_2)\phi_2p_3$. The number of animals released at period one exhibiting each of the four possible capture histories can again be modeled using the multinomial distribution.

The method of maximum likelihood can be used to estimate parameters ϕ_i and p_i of the Cormack and Jolly-Seber models. Jolly (1965) and Seber (1965) also showed how to estimate the number of animals (N_i) in the population at period i and the number of animals (B_i) entering the population between periods i and $i + 1$ and in the population at $i + 1$.

There have been a number of modifications to the Cormack and Jolly-Seber models in recent years. Some modifications have involved parameter constraints in which either survival probabilities or capture probabilities or both sets of parameters are modeled as constants that do not depend on sampling occasion (e.g., $p_i = p$, and/or $\phi_i = \phi$ for all i ; Brownie et al. 1986, Clobert et al. 1985, Cormack 1981, Crosbie and Manly 1985, Jolly 1982, Lebreton et al. in press, Pollock et al. 1990, Sandland and Kirkwood 1981).

The biologist often focuses on the many possible sources of variation in natural systems, and the development of constrained models may not appear to make sense at first glance. However, the rationale underlying development of constrained models is referred to as the principle of parsimony. The basic idea is that sampling variances increase with number of model parameters, so it is desirable to use the minimal number of parameters that adequately describe the variation in the data (see discussions in

Table 2. Possible capture histories and associated probabilities for animals caught in period one of a three-period study of an open population under the Cormack and Jolly-Seber models.

Capture history	Probability
111	$\phi_1 p_2 \phi_2 p_3$
110	$\phi_1 p_2 (1 - \phi_2 p_3)$
101	$\phi_1 (1 - p_2) \phi_2 p_3$
100	$(1 - \phi_1) + \phi_1 (1 - p_2) (1 - \phi_2 p_3)$

Burnham and Anderson in press, Lebreton et al. in press).

Other modifications to the Cormack and Jolly-Seber models have involved the addition of parameters to relax assumptions and increase generality. For example, Robson (1969), Pollock (1975), and Brownie and Robson (1983) considered models in which initial capture and marking have a temporary (usually one trap period) influence on capture and survival probabilities. Pollock (1981) and Stokes (1984) generalized the Jolly-Seber model to incorporate age-specificity of survival and capture probabilities. Reduced-parameter models incorporating age-specificity were then developed by Brownie et al. (1986; also see Pollock et al. 1990) and Clobert et al. (1987; also see Lebreton et al. in press).

Estimation for open populations is typically conducted using software developed specifically for that purpose (see review of available software in Lebreton et al. in press). Computer programs such as POPAN3 (Arnason and Schwarz 1986), CMR (Crosbie and Manly 1985), and JOLLY and JOLLYAGE (Pollock et al. 1990) compute estimates under several different models for open populations. Other software packages, such as SURVIV (White 1983) and SURGE 4.0 (Lebreton et al. in press), do not contain a preselected set of models but permit the user to specify models of interest. These latter programs require more knowledge by the user, but they permit the tailoring of analyses to specific field situations and are extremely powerful. Most recent software computes goodness-of-fit and between-model test statistics for use in selecting an appropriate model.

A final topic that merits mention here is the special class of open capture-recapture models known as band-recovery models. These models

were developed for the special case in which a marked animal is recaptured one time at most. The common application for these models is to populations that are hunted or fished. Recapture data, which come from hunters or fishermen or from conservation officers or wardens who check such people in the field, represent recoveries of dead animals; hence, animals may be recaptured only once. These models were developed in the 1970s (Brownie and Robson 1976, Seber 1970) and are summarized in Brownie et al. (1985). Programs BROWNIE and ESTIMATE (Brownie et al. 1985) and MULT (Conroy and Williams 1984, Conroy et al. 1989) compute estimates using selected sets of models, and SURVIV (White 1983) can be used to estimate parameters of user-defined models. It is also possible to use SURVIV to develop models for carrying out joint analyses of band recoveries (e.g., birds shot by hunters) and recaptures from a group of marked animals (Szymczak and Rexstad in press).

The robust design. Pollock (1982) noted that in many situations it would be advantageous to design capture-recapture studies so that both open and closed models could be used within the same study. The robust design includes l secondary sampling periods within each of k primary periods. The time interval between successive secondary periods within a primary period is short (e.g., we might trap small mammals for five consecutive days), hopefully permitting the use of closed population models on resulting data. Consecutive primary periods are separated by relatively long intervals (perhaps one or two months in the small-mammal example), and capture histories based on primary periods can be analyzed using open models.

The original motivation for this design was that estimates of population size based on open models can be badly biased if underlying model assumptions are not met, whereas there are numerous closed models (Otis et al. 1978, Rexstad and Burnham 1991, White et al. 1982) that permit estimation of population size in the presence of various sources of variation in capture probability. Open-model estimates of survival rate, how-

ever, are relatively robust (insensitive to deviations from underlying model assumptions). Pollock (1982) thus recommended estimating population size using capture histories over secondary periods in conjunction with closed models and survival rate using capture histories over primary periods using open models. Numbers of new recruits (B_i) to the population are then estimated by using survival estimates from open models and population-size estimates from closed models. Recent work has shown that the robust design also permits estimation of quantities that cannot be estimated using either closed or open models exclusively (Kendall and Pollock in press, Nichols and Pollock 1990, Nichols et al. in press).

From estimation to testing

Until the last 10–12 years, virtually all the model development in capture-recapture statistics was directed at estimating quantities such as survival rate and population size. Usually, however, biologists are not nearly so interested in the numerical value of these quantities as in comparisons of these quantities (e.g., among populations in different habitats or exposed to different environmental conditions or management schemes). In recent years, biostatisticians have thus turned their attention to testing hypotheses of biological interest.

Before the last decade, tests between different capture-recapture and band-recovery models were not uncommon. For example, users of program CAPTURE (Otis et al. 1978) used tests between the different closed population models to identify important sources of variation in capture probabilities (Otis et al. 1978). Users of some of the primary software packages for open population models used between-model tests to draw inferences about age- and time-specificity of survival and capture probabilities (Brownie et al. 1985, Clobert et al. 1985, Pollock et al. 1990, Sandland and Kirkwood 1981). However, the primary motivation for developing these models and tests was not so much to address questions of biological interest as to identify realistic, yet parsimonious, models for use in parameter estimation.

North and Morgan (1979) developed a band-recovery model in which the survival rate of first-year animals (grey herons) was modeled as a logistic function of an environmental variable (in this case, winter temperature and periods below freezing):

$$S'_i = (1 + e^{\alpha + \beta t_i})^{-1} \text{ (equation 5),}$$

where S'_i is the annual survival rate for first-year animals in year i , t_i is the value of the environmental covariate for year i , and α and β are model parameters to be estimated. The logistic model of equation 5 was incorporated directly into a band-recovery model, essentially by substituting $(1 + e^{\alpha + \beta t_i})^{-1}$ for S'_i every place in the model where the first-year survival parameter appeared, an approach known as ultrastructural modeling. Parameters α and β were thus estimated directly. Examination of the estimates of β and its standard error, $SE(\hat{\beta})$, and tests between the logistic model and models with no winter weather effects provided the basis for the inference that first-year survival of grey herons was lower during years with severe winters (North and Morgan 1979).

Frequently, estimation under ultrastructural models such as those of North and Morgan (1979) for band-recovery data is computationally intensive. Program SURVIV (White 1983) is extremely flexible and permits the user to model survival rate in terms of external covariates using a variety of possible functions. Program MULT (Conroy and Williams 1984, Conroy et al. 1989) was also written for band-recovery data and includes the ability to model survival rate as a linear function of a specified covariate.

Anderson et al. (1982), Burnham et al. (1984), and Barker et al. (1991) used an ultrastructural-model approach to investigate the relationship between hunting mortality rate and annual survival rate in duck populations. This modeling approach differs from that of North and Morgan (1979) in that it uses no external covariate. Instead, annual survival rate is modeled as a function of band-recovery rate, a parameter estimated from the same data used to estimate survival. These analyses, like those of North and Morgan (1979) and Conroy and Williams (1984), involve

band-recovery models, and estimation is accomplished by using program SURVIV (White 1983) and MULT (Conroy et al. 1989).

Although the initial modeling work with covariates was done in the context of band-recovery models, Clobert and Lebreton (1985) extended this approach to the more general capture-recapture models for open populations. They developed software (SURGE) to compute estimates and test statistics under such models and used this software to investigate questions regarding the influence of winter temperature, density of conspecifics, and density of presumed competitors on survival rates for different animal populations (Clobert and Lebreton 1985, Clobert et al. 1987, Lebreton et al. in press).

Although of less biological interest, various measures of recapture and resighting effort have also been used as covariates in capture-recapture models for both closed (Pollock et al. 1984) and open (Clobert et al. 1987, Lebreton et al. in press) populations. For example, Clobert et al. (1987) estimated survival rates of black-headed gulls using resightings obtained from a floating blind. Annual sighting probability was modeled as a function of time spent in the floating blind, which varied from year to year (Clobert et al. 1987). This ultrastructural modeling of sighting probability reduced the number of parameters in the overall model, thus yielding more precise estimates of annual survival rates.

These covariate analyses (e.g., North and Morgan 1979, Lebreton et al. in press) address possible associations between time-specific survival (or capture) probabilities and covariates that also exhibit temporal variation. These analyses are typically conducted with data from a single population extending over a number of periods. However, recent work has also been directed at the use of capture-recapture data to compare survival probabilities for two or more populations over the same period(s).

The comparison of survival rates for two or more groups of marked animals was considered in detail by Burnham et al. (1987). The initial motivation for this work was experiments on fish mortality associated with hydroelectric dams. They considered the situation in which one group of marked fish is released

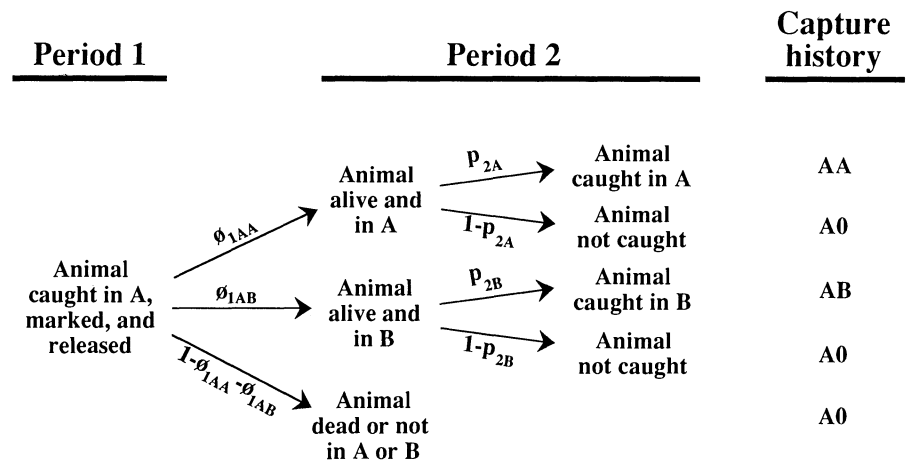


Figure 2. Diagram of events and associated probabilities for an animal released in location A in period one of a two-location, two-period study under the Arnason model for spatially stratified open populations.

above a dam and another group below the dam at the same time. Fish from both groups are then recaptured at downstream dams, and resulting recapture data permit estimation of the mortality associated with passing through the dam turbines.

The modeling of the data by Burnham et al. (1987) is based on the Cormack and Jolly-Seber models, and the different models used in hypothesis testing are defined by the numbers and types of parameters (e.g., time-specific capture and survival probabilities) shared by the two groups of fish. For example, the effect of primary interest is a difference in the probability of surviving from the time of release until reaching the first downstream dam (or other sampling station). In some situations, it is reasonable to expect probabilities of surviving between subsequent dams or sampling stations and of being recaptured at these stations to be identical for the two groups of fish. We can thus test for the initial survival difference via a test between models representing the alternative (first survival probability differs between the two groups of fish, whereas all other survival- and capture-probability parameters are the same for the two groups) and null (all parameters, including the first survival probability, are the same for the two groups of fish) hypotheses.

The computer program RELEASE was developed for use in experiments of this sort, and it can be used to compare survival and capture proba-

bilities for two or more groups of released animals (Burnham et al. 1987). RELEASE fits a series of models beginning with a model in which all parameters are different for the two groups and moving to models in which progressively more parameters are shared. For certain problems with multiple data sets, it may be desirable to fit models other than those in RELEASE. Programs SURVIV and SURGE are flexible and can be used to implement models not incorporated in RELEASE (Burnham et al. 1987, Lebreton et al. in press).

In addition to the fish mortality experiments, this model-based approach to comparing multiple data sets has been used in conjunction with dosing experiments involving lead pellets in ducks and pesticides in nestling starlings and with density manipulations (animals were removed from one study plot and added to another) in lizard populations (Burnham et al. 1987, Lebreton et al. in press). Such comparisons have also been used to address questions about whether survival and/or capture probabilities are associated with characteristics, such as sex, age, and body mass, that are not experimentally induced (Krementz et al. 1989, Lebreton et al. in press).

In addition to comparing survival and/or capture probabilities among study populations, the biologist is sometimes interested in comparing population size. Skalski and Robson (in press) consider methods of testing

hypotheses about differences in population size using capture-recapture estimators for closed populations.

Movement and multiple states

Animal ecologists are becoming increasingly aware of the importance of immigration and emigration to animal population dynamics, but this awareness has not translated into much work by capture-recapture statisticians. Two-sample capture-recapture studies on geographically stratified populations were investigated by Chapman and Junge (1956) and Darroch (1961). Arnason (1972, 1973) considered the extension of the Jolly-Seber model for open populations to two or more areas, but this model saw little use until recently (Hilborn 1990, Hestbeck et al. 1991).^{1,2}

Capture history notation for open models incorporating movement is similar to that described previously for open models in that columns denote sampling periods and 0s denote no capture. However, instead of using 1s to denote capture, captures are denoted by capital letters, with different letters indicating different locations at capture. For example, A0B would denote an animal caught in location A in sampling period one, not caught in period two, and caught in location B in sampling period three.

We also add subscripts to model parameters to specify location. Let p_{ij} denote the probability that an animal in area j at time i is captured or sighted in that period. Let ϕ_{ijk} denote the probability that an animal alive and in location j at period i is alive and in location k at period $i + 1$. Just as in the case of a single study area, we can model the events leading to each possible capture history (Figure 2, Table 3). The parameter ϕ_{ijk} represents the product of a survival probability and a movement probability, and under certain reasonable assumptions (e.g., that survival between i and $i + 1$ depends on location at i but not

Table 3. Possible capture histories and associated probabilities for animals released in location A at sampling period one of a two-period, two-location study of an open population.

Capture history	Probability
AA	$\phi_{1AA}p_{2A}$
AB	$\phi_{1AB}p_{2B}$
A0	$1 - \phi_{1AA}p_{2A} - \phi_{1AB}p_{2B}$

at $i + 1$, a standard assumption in capture-recapture estimation), these probabilities can be estimated separately (Hestbeck et al. 1991).

These models with geographic stratification have been applied to skipjack tuna in the western Pacific (Hilborn 1990), Canada geese in eastern North America (Hestbeck et al. 1991), and Pacific herring off the coast of Canada.³ The Arnason model of Figure 2 and Table 3 is Markovian in the sense that movement between periods i and $i + 1$ depends only on location at i (e.g., where we find an animal this winter depends on where it was last winter; locations in previous winters are irrelevant). This assumption was found to be unrealistic for Canada geese, so an additional memory model was developed in which movement between winters i and $i + 1$ depends on location at both i and $i - 1$ (Hestbeck et al. 1991). This latter model provided an adequate description of the Canada goose resighting data. A FORTRAN program is available from Schwarz and colleagues⁴ to obtain estimates under some movement models, and Brownie and colleagues⁵ have written a routine for SURVIV permitting estimation under the Arnason model, the memory model of Hestbeck et al. (1991), and various reduced-parameter models.

Although the Arnason and related models were developed with geographic stratification in mind, they provide the appropriate framework for other kinds of stratification as well. For example, Kremetz et al. (1989) stratified nestling starlings by weight on day 18 after hatching and used RELEASE to test for differences in survival and capture probabilities of heavy versus light birds over a several-week study period. However, weight is a characteristic likely to change over

time, and in a long-term study it would not be reasonable to use weight at one point in time (e.g., the initial sampling period) as the basis for stratification over the entire study.

One approach to dealing with such change is to use the Arnason model with weight, rather than location, as the basis for stratification (Nichols et al. in press). Animals may then move among different strata, and stratum-specific survival and capture probabilities can be estimated. These models may be used in conjunction with any state variable that can be assessed at the time of capture (location, weight, reproductive activity, or behavior) and are thus well-described by the term *multistate models*. Such models provide the framework for testing hypotheses of ecological interest such as the cost of reproduction and the relationship between physiological state and survival.

Reproduction

All changes in population size are the result of survival, movement, and reproduction, and there has been some work on estimating reproduction variables from capture-recapture data. The Jolly-Seber \hat{B}_i estimates the number of animals recruited into the population between sampling periods, and Crosbie and Manly (1985) consider ways of modeling this recruitment. It is possible to decompose the Jolly-Seber \hat{B}_i into components associated with immigration and in situ reproduction (Nichols and Pollock 1990, Pollock et al. 1990). When considering the use of the Jolly-Seber recruitment estimator, it is important to remember that \hat{B}_i and estimates of its components are typically imprecise (have large sampling variances) relative to Jolly-Seber estimates of survival rate and population size (Pollock et al. 1990).

Lebreton et al. (1990) and Clobert et al. (1990) have recently developed capture-recapture models for estimating age-specific breeding proportions. The multistate models also permit estimation of breeding proportions and provide a framework for addressing questions about transitions between breeding and nonbreeding states (e.g., does the probability of breeding in year i depend on whether the animal bred in year $i - 1$?).

¹C. Brownie, J. E. Hines, J. D. Nichols, K. H. Pollock, and J. B. Hestbeck. 1992. Manuscript in review. Department of Statistics, North Carolina State University, Raleigh, NC 27695-8203.

²C. J. Schwarz, J. F. Schweigert, and A. N. Arnason. 1992. Manuscript in review. Department of Statistics, University of Manitoba, Winnipeg, Manitoba R3T 2N2, Canada.

³See footnote 2.

⁴See footnote 2.

⁵See footnote 1.

Other applications

Capture-recapture models have been used for other applications in animal population ecology that do not use marked animals, such as efforts to estimate the sampling fraction in surveys of inanimate objects (e.g., animal nests). For example, aerial surveys of crocodilian nests can be conducted by two different observers, with each observer marking nest locations on a map or aerial photograph. The nests seen by observer one can be denoted as n_1 , those seen by observer two as n_2 , and those seen by both observers as m_2 . The Lincoln-Petersen estimator (equation 4) then provides an estimate of the total nests in the searched area (see Magnusson et al. 1978).

In ground surveys of nests or other animal structures, observers independently search and place marks (e.g., metal washers with a different color for each observer) inside nests that are located. After all observers have completed the survey route, they go over the area once again locating nests and recording the colors of washers found in each nest. The number and identity of observers who found each nest then represent the nest's capture history, and closed population models can be used for estimation (e.g., Nichols et al. 1986).

Community ecologists are frequently interested in species richness (the total number of species within some group of interest inhabiting a particular area). The frequency distribution of number of species for which 1, 2, 3, . . . , n individuals are encountered during sampling efforts (capture or observational methods may be used for sampling) can be used in conjunction with certain closed population models to estimate the number of species not encountered during sampling and, hence, species richness (Burnham and Overton 1979, Efron and Thisted 1976).

Animal ecologists have a tradition of borrowing quantitative methods from workers in other disciplines, such as physicists and human demographers. It is interesting that capture-recapture models developed by animal ecologists provide the appropriate framework for estimation problems in other fields (Pollock 1991). In the biological sciences, these models have been used with fossil data to estimate

taxonomic diversity and rates of extinction and origination (Nichols and Pollock 1983). The Bureau of the Census uses these models to estimate the undercount (Wolter 1986). Capture-recapture models have also been used to estimate the size of other hidden human populations, such as those involved in various types of criminal activities, those with particular illnesses, and those within a city who are homeless (e.g., Sudman et al. 1988).

Remote-sensing data from multiple spectral scanners can be used with capture-recapture models to estimate the number of animals and other kinds of objects (Anderson et al. 1986). Data on the location of specific errors found in computer programs and manuscripts by different examiners and proofreaders can be used to estimate the total number of errors (e.g., White et al. 1982). These models have even been used to estimate the number of words that Shakespeare knew and to decide whether newly discovered works can be attributed to him (e.g., Efron and Thisted 1976).

Conclusions

Recent advances in capture-recapture modeling, including the biologically motivated emphasis on model-based hypothesis testing and the development of models for spatially stratified populations, have the potential to revolutionize the conduct of field studies in animal ecology. The burden now falls to the animal ecologist to incorporate these advances in his or her work. Historically, those of us who study animal populations have been slow to recognize the utility of capture-recapture advances and to make good use of them. We have instead fallen back on ad hoc approaches that ignore the severe problems associated with count statistics reflecting unknown sampling fractions.

Recent work by capture-recapture statisticians has produced user-friendly software that runs on personal computers and that can provide estimates and model test statistics under a variety of sequences of standard models in seconds. For nonstandard problems, flexible software is now available that permits the user to tailor models to specific sampling situa-

tions. This software should reduce the historical time lag between model development and use and result in the rapid assimilation of new capture-recapture models into the field of animal population ecology.

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