

(see also Paulik and Robson [14]). The population proportion of type x before the removal is $P_1 = X_1/N_1$, where X_1 is the population size of type x , and N_1 is the population size of both x and y types. We remove (often by fishing or hunting) a known number of animals of each type, R_x and R_y , with total removals $R = R_x + R_y$. This means that the proportion of type x after the removal (P_2) is

$$P_2 = \frac{X_2}{N_2} = \frac{X_1 - R_x}{N_1 - R} = \frac{P_1 N_1 - R_x}{N_1 - R}$$

Typically R_x and R are assumed known, but they could be estimated separately. We can obtain estimates of P_1 and P_2 from some kind of survey of the population before and after the removal; then the only unknown in the equation is N_1 , and by rearrangement we obtain the estimator

$$\hat{N}_1 = \frac{R_x - R\hat{P}_2}{\hat{P}_1 - \hat{P}_2}$$

Other estimators can be derived from this: $\hat{X}_1 = \hat{P}_1 \hat{N}_1$, $\hat{N}_2 = \hat{N}_1 - R$, and $\hat{X}_2 = \hat{X}_1 - \hat{R}_x = \hat{P}_2 \hat{N}_2$. (Also the *exploitation rate* $u = R/N_1$ can be estimated and is very important to managers.)

Using the delta method (*see* STATISTICAL DIFFERENTIALS), the variance estimators are seen to be

$$\text{Var}(\hat{N}_1) = (P_1 - P_2)^{-2} [N_1^2 \text{Var}(\hat{P}_1) + N_2^2 \text{Var}(\hat{P}_2)]$$

and

$$\text{Var}(\hat{X}_1) = (P_1 - P_2)^{-2} [N_1^2 P_1^2 \text{Var}(\hat{P}_1) + N_2^2 P_1^2 \text{Var}(\hat{P}_2)].$$

The variance of \hat{N}_2 is the same as that of \hat{N}_1 , and of \hat{X}_2 the same as that of \hat{X}_1 .

The precision of the estimators of N_1 and X_1 depends on the initial proportion P_1 , the size of the induced difference ($P_1 - P_2$), and the number of animals that are observed or captured in the surveys to estimate P_1 and P_2 . In general, the CIR method gives precise estimates when $P_1 - P_2$ is large, i.e., when the removal is large and highly selective (Paulik and Robson [14], Seber [19], Pollock et al. [17], Conner et al. [4]). Nonsensical estimates can result if the population composition is little changed by the removal.

CHANGE-IN-RATIO ESTIMATORS

Change-in-ratio (CIR) methods provide estimators of population parameters (population size, harvest rate, productivity, survival rates, etc.) for fish and wildlife* populations based on changes in proportions of population subclasses before and after known selective removals. They are potentially useful because the required data are often relatively easy to obtain. For example, a male snow crab population might be subject to a carefully monitored fishery which only removes the large crabs (larger than 95 mm). Research surveys before and after the fishing season could measure the change in the proportion of large crabs in the population (Dawe et al. [5]).

The CIR method was developed in the 1940s for wildlife studies (Kelker [10]) and has been refined since then. Reviews are given by Paulik and Robson [14], Seber [19], Pollock [16], and Lancia et al. [11]. The CIR method is closely related to capture-recapture* methods, which have a much longer history (see for example Seber [19]) going back to Laplace [12], who used a variation of the two-sample capture-recapture method to estimate the population of France.

TWO TYPES, ONE REMOVAL (TRADITIONAL CLOSED-POPULATION MODEL)

The traditional CIR procedure for a *closed* (i.e. constant) population with two types of animals (x and y) and one removal is now described using the notation of Seber [19, p. 353]

Like all methods of estimating animal abundance, the CIR method requires strong assumptions. These are:

1. total closure of the population, except for the removals,
2. that the removals are known exactly, and
3. that the probability of sighting or capturing animals of each type is the same for each survey.

The first assumption, population closure, is crucial. There can be no recruitment, mortality, immigration, or emigration during the study, so that the only change in the population between surveys is the removals. This assumption may be reasonable if the hunting or fishing season is short.

Ideally, the removals should be known exactly, but precise estimates will do. The variance equations for \hat{N}_1 and \hat{X}_1 have to be modified in this case (see for example Dawe et al. [5]). Clearly the estimators will have higher precision when the removals are known exactly.

The third assumption of equal sightability or catchability of types of animals in the surveys is the most difficult to meet in practice. Male deer may be less visible than female deer (Lancia et al. [11]), for example, or larger fish may be easier to capture in fishing gear than smaller fish. Models which relax this assumption are discussed in the next section. An unbiased estimate of X_1 is possible if only x -type are removed, even if catchabilities of the two types are unequal (Seber [19, p. 353]).

Conner et al. [4] applied the traditional CIR model to the white-tailed deer population in and around Remington Farms, Maryland, USA, in 1980–1981. Pre-hunt and post-hunt roadside counts gave the proportion of antlered deer to be $\hat{P}_1 = 0.0963$ and $\hat{P}_2 = 0.0381$ respectively. During a one-week hunt $R = 110$ deer were killed, and of these $R_x = 56$ were antlered. From this information $\hat{N}_1 = 890$ is the estimate of the total deer population, with $\hat{X}_1 = 86$ antlered deer in the population. After the hunt, $\hat{N}_2 = 890 - 110 = 780$ and $\hat{X}_2 = 86 - 56 = 30$. The standard error of \hat{N}_1 was 149, which is about 20% of the estimate. The

first two assumptions appeared to be valid, but because the antlered deer were less observable than the antlerless, Conner et al. [4] believed their estimates of population size were biased high.

EXTENSIONS OF THE CLOSED POPULATION MODEL

Otis [13] developed a model for the case where there are *three types* of animals. He made basically the same assumptions, except that now he assumed that all animals of each of the three types were equally sightable in each of the samples. Examples of three types are young, yearling, and adult animals or young, female adult, and male adult animals. In an important work, Udevitz [20] realized that it is possible to generalize to *three or more types* of animals and allow for some degree of unequal sightability or catchability of different types at each sampling time. Specifically, he showed that it is sufficient to assume that two types have equal catchability and that the ratios of sightabilities of the other types to those of the first two are constant over sampling times. He provides ML estimators and likelihood ratio tests* for a variety of models.

Chapman [1] considered ML estimates for a model where the closed population had two types but was subject to two different known selective removals. He kept the assumption that both types had the same probability of being sighted in a sample. In this case, there is a need to estimate the proportion of type x at three sampling times. For this case, Pollock et al. [17] showed that it is possible to allow sighting rates to differ by type at each sampling time, provided the ratio of sighting rates is constant for the three times. They concentrated on the special case in which only type x was removed first and type y removed second; however, they showed that estimation was possible in the more general case. Udevitz [20] considered a range of models for which there are *several removals* and *several types*. These models have great potential, but substantial rates of removal appear to be necessary for the estimators to behave well. These methods deserve further develop-

ment and application to real populations. (See also Udevitz and Pollock [21, 22].)

Heimbuch and Hoenig [8] developed a model for a closed population divided into spatial regions. The objective is to estimate proportions of the population that occur in each region. The model is based on the following assumptions: (1) catch rate is proportional to abundance, (2) sampling gear efficiencies are constant over time but possibly variable among regions, (3) the population is closed, and (4) the proportion of the population within each region changes during the study. Changes in observed catch rates are assumed due to a redistribution of the population among regions, because of the closure assumption.

ESTIMATING RELATIVE SURVIVAL RATES

Paulik and Robson [14] showed that the ratio of survival rates for two types x and y can be estimated from the ratios of abundances at two times. Thus

$$[S_x/S_y] = \hat{r}_2/\hat{r}_1,$$

where S_x and S_y are the survival rates for x - and y -type animals, respectively, between times 1 and 2, and where \hat{r}_i is an estimate of the ratio of abundances of types $x:y$ at time i . The catchabilities of the two types need not be equal or constant over time, provided the ratio of catchabilities remains constant. Hoenig et al. [9] showed that the generalization of this to more than two samples is a logistic regression. They estimated the relative survival of late- and early-spawned fish larvae.

OPEN-POPULATION MODELS

Chapman and Murphy [2], in a very important paper, present a CIR model which allows for natural mortality as well as exploitation (the removals). Their model allows estimation of population sizes, survival rates, and exploitation rates ($u = R/N_1$). They consider special cases for instantaneous and continuous removals.

Open models (i.e. models which allow for mortality and emigration, recruitment, and

immigration) have not been studied much, especially in recent years. For early work, see Hanson [7], Chapman and Murphy [2], and Paulik and Robson [14]. Seber [19, p. 381] gave a brief review. Further research could be important and should consider extensions along the lines of Udevitz [20] for closed-population models, allowing for varying degrees of unequal catchability of types. Models allowing for recruitment could probably also be developed if a series of closed CIR models were used in different years or if CIR were combined with capture-recapture of tagged animals.

COMBINING CIR WITH OTHER METHODS

Chapman [1] noted that CIR may be combined with capture-recapture data for a closed model. We believe that this work could be extended to more general closed models and to open models. Dawe et al. [5] showed that CIR may be combined with the index-removal method (Petrides [15], Eberhardt [6]). Research on combining CIR, index-removal, and removal (Seber [19, p. 296]) data has been conducted by Chen [3].

RELATIONSHIP WITH CAPTURE-RECAPTURE

Rupp [18] pointed out that the Petersen capture-recapture estimates (see for example Seber [19, p. 59]) is a special case of the traditional CIR estimator presented earlier. Let X and N denote the marked and total populations respectively. At time 1, $X_1 = 0$ and hence $P_1 = 0$. There is an addition of M marked animals, so that $R_x = -M$, and a removal of unmarked animals, so that $R_y = +M$, with the total removal $R = R_x + R_y = 0$. This means that

$$\hat{N}_1 = \frac{R_x - R\hat{P}_2}{\hat{P}_1 - \hat{P}_2} = \frac{M}{\hat{P}_2}.$$

Now $\hat{P}_2 = m/n$ is the usual estimate from capture-recapture sampling at time 2, so that $\hat{N}_1 = Mn/m$, the usual form of the Petersen estimator.

CONCLUSION

The CIR method has not been used very much in practice; however, we expect this will change in the future. Recent theoretical developments have made the models more realistic. Also, the current emphasis in development of modern methods of estimating abundance of animal populations is the combination of more than one approach to allow model checking and increased precision. CIR is thus one easy-to-apply method that could be combined with index-removal, removal, catch-effort, or capture-recapture methods.

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(ADAPTIVE SAMPLING
CAPTURE-RECAPTURE
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TRANSECT METHODS
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KENNETH H. POLLOCK
JOHN M. HOENIG

CHANGE-OVER TRIALS See CHANGE-OVER DESIGNS; CROSSOVER TRIALS