CHAPTER 4
REMOVAL METHODS

When our goal is to estimate population size, it is logical to want to do a one-time only, 100% count of the population. In theory, a 100% count can be achieved by a removal study; that is, as each individual is caught it is removed from the population, either permanently or for the duration of the study. Thus, additional captures must represent different individuals. By extending the capture effort until no more individuals are caught, we should obtain a 100% count. Unfortunately, there are practical problems with this approach, just as there are with the capture-recapture method. In this chapter we discuss the modeling, data analysis, and advantages and disadvantages of the constant-effort removal method.

Electrofishing in ponds, small lakes, or small streams with a flow of only 0.1 to 1 cubic meters per second is the most common example of the removal method. For an introduction to the literature on this subject see *Friedman (1974)*, and *Seber (1982)*. Usually, the fish are not killed; rather, they are removed when they are caught, held until the end of the several removal passes, and then returned to the pond, lake, or stream. One removal occasion usually consists of a complete pass, going first upstream and then downstream in the study area. At least two such passes should be made, and we maintain that three or more are necessary unless the efficiency of the gear is very high—that is, unless the capture probability is 0.8 or more on each pass. Equal effort is required on each pass for the models presented here. In the optimal situation, 100% of the fish are removed in the first pass; the second pass is made to verify that all fish have been counted. In practice, capture probabilities as high as 0.8 are uncommon (although this may be a reflection of the electrofishing gear in use), and significant numbers of fish will be caught on the second and subsequent passes.

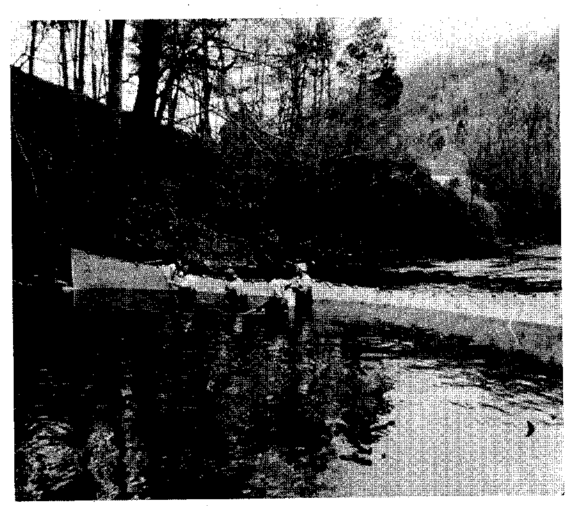
Removal sampling of small mammals is usually accomplished with snap traps. However, simply removing live-trapped animals from the area would suffice. In fact, neither removal from the area nor kill trapping is necessary to apply removal analysis methods to trapping data for small mammals. Initially, all animals in the population at risk of capture are unmarked, or their marks are known to be from an earlier trapping effort. Animals can be captured, marked, and released, and we can think of them as removed from the unmarked population segment; *Seber (1973:323)* has referred to this approach as "removal by marking." Thus, by using only first captures in a live-trapping study, we can analyze the data as a removal study.

The removal method circumvents any behavioral response to trapping during the study. (We define behavioral response as a change in capture probability after, and as a result of, first capture.) In fact, as mentioned in Chapter 3, the data from capture-recapture models M_b and M_{bh} are properly analyzed as removal studies because of this dominant behavior effect. If killing the animal is tolerable, a removal study on small mammals is quicker and cheaper than a live-trapping study. No tags are needed, kill traps are cheaper, handling the animals is easier, and on successive occasions fewer animals are caught so less field time is required.

The immediate and major disadvantage of physically removing the animals is that geographic closure is usually violated—after a few days, individuals originally too far from the grid to have been caught will start moving into the area vacated by the removals. Also, there is the obvious disruption of the local population, so the method is not suitable for studies to be repeated in the near future.

Electrofishing in a Virginia stream. Notice the generator in the boat and the lead to an electrode. (Photograph courtesy of R. F. Raleigh.)

Working the two electrodes during electrofishing in a Virginia stream. (Photograph courtesy of R. F. Raleigh.)



A net is used to close off the lower end of the sampled stream during electrofishing in a Virginia stream. (Photograph courtesy of R. F. Raleigh.)

The Removal Model, Assuming Constant Capture Probability

The Model and Its Assumptions. In the simplest removal model, every individual has an equal and constant probability of capture on all removal, or capture, occasions. This is the model most often encountered in the literature *(Hayne 1949a; Moran 1951; Zippin 1956, 1958; Seber and Whale 1970; Otis et al. 1978:28-32, 107-108; and Seber 1982)*. To illustrate the model, we consider a population of size $N = 625$, with every individual having an independent, unchanging probability of capture of $p = 0.4$. On the first capture occasion, the expected number of captures is 250 ($= 625 \times 0.4$), which leaves 60% of the population (375) uncaught. On the second occasion, the expected number of captures is 40% of the remaining 375 animals, or 150 ($= 375 \times 0.4$). The expected (average) data from four capture occasions shown in Table 4.1 continue the argument. Even after four occasions, we can expect an average of 81 individuals to remain uncaught.

This model has only two parameters: population size N and capture probability p. The only data from removal sampling are the numbers of captures on each of t capture occasions; we let $u_1, \ldots, u_t$ represent these data. If $E(u_j)$, $j = 1, \ldots, t$ represents the expected (average) number of captures on occasion j, the constant-effort removal model for $E(u_j)$ is

$$E(u_j) = N(1-p)^{j-1}p, \qquad j = 1, \ldots, t.$$

Thus, $E(u_1) = Np$ for occasion 1; $E(u_2) = N(1-p)p$ for occasion 2; and $E(u_t) = N(1-p)^{t-1}p$ for the final occasion. Our understanding of this model can be tested by computing the elements of Table 4.1. For example, $E(u_4) = 625(1-0.4)^3(0.4) = 625 \times 0.216 \times 0.4 = 54$.

P. A. P. Moran

The contributions made to removal sampling and analysis methods by P. A. P. Moran were somewhat fortuitous. After World War II, he worked at the Institute of Statistics at Oxford. The Institute was housed in the same quarters as the Bureau of Animal Population under Charles Elton. Moran, through friendships with both Elton and P. H. Leslie, became interested in animal populations and estimation in removal experiments.

Moran was born in 1917 and educated at the Universities of Sydney and Cambridge. His interests over the past 30 years have turned in other directions. He is currently in the Statistics Department at the Australian National University, Canberra, Australian Capital Territory. (Recent photograph.)

TABLE 4.1. Expected (average) results of a removal study on a population of size N = 625 with equal, independent capture probability of p = 0.4 for all individuals and t = 4 removal occasions.

Removal Occasion, j	Population Size At Start Of Occasion	Expected Number Captured, E(j)	Number Not Yet Caught
1	625	250	375
2	375	150	225
3	225	90	135
4	135	54	81

The assumption of equal effort is necessary if the capture probability is to be the same on every capture occasion. In electrofishing studies, the equal effort requirement demands the use of a standardized technique on each occasion. It is especially important to prevent a letdown of effort after the first pass. In trapping small mammals, the same number of operating traps is required on each occasion, and the same length of time must intervene between setting the traps and checking them on each occasion.

The usual assumption for removal studies does not allow heterogeneity of capture probabilities. That is, there can be no innate differences in capture probabilities. However, the assumption fails to some extent in electrofishing because capture probabilities are related to the size of the fish. In trapping small mammals, capture probabilities may vary by species, age, or sex of animals. In both types of studies, a solution to the problem is to separate the data by size-class of fish (within broad limits) or by species, age, or sex of animal and to analyze each data subset separately. An example showing a partitioning of data by the sex of the animal appears in Chapter 6.

Some Simulated Data. In real applications, the data are subject to sampling variations; therefore, the numbers of animals captured will not decrease as smoothly as those shown in Table 4.1. An actual application is more likely to produce results like those shown in Table 4.2, where simulated data are given, based on the same model as Table 4.1 (N = 625 and p = 0.4). The numbers caught are not calculated in a deterministic manner; rather, they are the realization of a random process. For example, on the first occasion the number caught is a random (binomial) variable with an expected value of 250 ($= N \times p$) and a sampling variance of 150 [$N \times p \times (1 - p)$]. Hence, the captures on the first occasion have a sampling standard deviation of 12.2 ($= \sqrt{150}$). Thus, for reasons rooted in mathematical statistics, we expect the number of individuals caught on the first occasion to fall between about 225 and

TABLE 4.2. A simulated instance of removal data on a population of N = 625 with equal, independent capture probability of p = 0.4 for all individuals and t = 4 removal occasions.

Removal Occasion, j	Population Size At Start Of Occasion	Number Captured, u_j	Number Not Yet Caught
1	625	260	365
2	365	141	224
3	224	97	127
4	127	50	77

275. With a more detailed analysis of this statistical model, we can predict the properties of the data for any values of N, p, and t.

Estimation for the Case $t = 2$. Given removal data like those shown in Table 4.2, we need an estimator of N. An acceptable, simple, closed-form estimator is available only for data from two ($t = 2$) occasions; it is not, however, the maximum likelihood (ML) estimator. For three or more occasions, efficient estimation becomes more complicated. We recommend using the exact ML estimator of N for any value of t. We also strongly recommend at least three sampling occasions, because the model's basic assumption (equal capture probability on every occasion) cannot be tested if $t = 2$. Of course, if capture probabilities are around 0.95, or even 0.9, two occasions will suffice, but such high capture probabilities are rarely achieved.

Because the ML estimator does not exist in closed form, numerical iterative techniques are required to compute it, even for $t = 2$. Program CAPTURE is available to perform these computations; we recommend that biologists use it to obtain the exact ML estimates for use with removal data.

For $t = 2$, a good approximation to the exact ML estimator is

$$\hat{N} = \frac{u_1}{1 - (u_2/u_1)} \quad . \tag{4.1}$$

Using the "data" of Table 4.1 to illustrate this formula, we have $u_1 = 250$, $u_2 = 150$, and hence

$$\begin{aligned}\hat{N} &= \frac{250}{1 - (150/250)} \\ &= \frac{250}{1 - 0.6} \\ &= \frac{250}{0.4} \\ &= 625 \quad .\end{aligned}$$

In this example we obtain the exact result of 625 because the data are the expected (average) numbers of removals under the model with $N = 625$ and $p = 0.4$. That is, they are not real data, subject to random variation. Using the simulated data of Table 4.2, we have $u_1 = 260$, $u_2 = 141$, and hence

$$\begin{aligned}\hat{N} &= \frac{260}{1 - (141/260)} \\ &= \frac{260}{1 - 0.542} \\ &= \frac{260}{0.458} \\ &= 568 \quad .\end{aligned}$$

A formula for estimating the sampling variance of the estimator in Eq. (4.1) is given in *Otis et al. (1978:108)*. This estimate is computed automatically by program CAPTURE for $t \geq 2$. For the above example, the estimated sampling variance of $\hat{N}$ is 2687.2 [$= \hat{var}(\hat{N})$]. The estimated standard error of $\hat{N}$ is thus $\hat{se}(\hat{N}) = 51.8$ ($= \sqrt{2\,687.2}$). Finally, for this example, an approximate 95% confidence interval on the true population size N is $568 \pm 1.96 \times 51.8$, or 466 to 670. The parameter p also has a simple estimator for the case $t = 2$. In fact, $\hat{p} = 1 - (u_2/u_1)$; thus, in the above example, $\hat{p} = 0.458$.

Figure 4.1 shows part of the output from program CAPTURE, giving the ML estimate for the same example with $t = 2$. In the figure, the ML estimates are $\hat{p} = 0.463605$ and $\hat{N} = 562$. (Two significant digits suffice in reporting such results.) These results are only slightly different from those of the closed-form formulas (Eq. 4.1). In the same figure, the estimated sampling standard error of the ML estimate of N is 50.0; in comparison, the estimated sampling error of the estimate of N derived from Eq. (4.1) is 51.8. The same formula is used to estimate the standard errors of both the $\hat{N}$ given by Eq. (4.1) and the ML estimate of N computed by CAPTURE. These sampling variance estimates are different only because the estimates of N and p differ slightly when the exact ML estimate is used instead of the closed-form formula.

We do not deal with the instance of only two removals in greater detail because we recommend using three or more capture occasions for two reasons: (1) three or more occasions are required to test the assumption of constant capture probability (that is, to perform a goodness of fit test of the model), and (2) a large gain in precision is achieved by making the extra effort of one or two additional passes. The case of two removals has been studied in considerable detail (see for example, *Seber and Whale 1970; Seber 1982*).

Estimation and Goodness of Fit Testing for Three or More Capture Occasions

We can recommend no closed-form estimators of N and p for $t \geq 3$. Figure 4.2 presents output from CAPTURE giving the ML estimates for the complete removal data of Table 4.2; that is, $t = 4$ rather than $t = 2$. In Fig. 4.2, $\hat{p} = 0.413609$, $\hat{N} = 621$, and the estimated standard error for $\hat{N}$ is 16.9401. Contrast these results with those for $t = 2$ in Fig. 4.1, especially the substantial improvement in precision when $t = 4$. From Fig. 4.1, we see that $\hat{se}(\hat{N}) = 49.95$ for $t = 2$, whereas from Fig. 4.2, we find that $\hat{se}(\hat{N}) = 16.94$ for $t = 4$. This change is a threefold improvement in precision of the estimate of N and is apparent in the point estimates of N. The true value of N is 625. For $t = 2$, $\hat{N} = 562$ and the error is -63, but for $t = 4$, $\hat{N} = 621$ and the error is only -4. In both examples, the approximate 95% confidence interval includes the true value of 625. The gain in precision with four capture occasions is substantial when capture probability is less than (about) 0.7, as this example illustrates.

If three or more capture occasions are used, there is a goodness of fit test for this constant capture probability model. It is a chi-square test of form (Observed $-$ Expected)^2/Expected, and Program CAPTURE computes this test. For the full data of Table 4.2, the test statistic value is 1.568 (based on 2 df); if the model is true, the probability of a value this large or larger is 0.4567. We conclude that the constant capture probability model fits the data of Table 4.2.

```
OCCASION           J=       1    2
TOTAL CAUGHT    M(J)=       0  260  401
NEWLY CAUGHT    U(J)=     260  141

ESTIMATED PROBABILITY OF CAPTURE, P-HAT =   0.463605

POPULATION ESTIMATE IS         562 WITH STANDARD ERROR      49.9536

APPROXIMATE 95 PERCENT CONFIDENCE INTERVALS          464 TO          660
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Fig. 4.1. Exact ML estimate of N as computed by CAPTURE by using the first two capture occasions in Table 4.2. The data are simulated from a true population of size N = 625 and p = 0.4.

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OCCASION           J=       1    2    3    4
TOTAL CAUGHT    M(J)=       0  260  401  498  548
NEWLY CAUGHT    U(J)=     260  141   97   50

ESTIMATED PROBABILITY OF CAPTURE, P-HAT =   0.413609

POPULATION ESTIMATE IS         621 WITH STANDARD ERROR      16.9401

APPROXIMATE 95 PERCENT CONFIDENCE INTERVALS          587 TO          655
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Fig. 4.2. Exact ML estimate of N as computed by using all four capture occasions in Table 4.2. The data are simulated from a true population of size N = 625 and p = 0.4.

Given the output of Fig. 4.2, we can compute the goodness of fit test on a hand calculator; we illustrate the computation as follows. First, we compute the estimated expected number of captures on each occasion; the formula is

$$\hat{E}(u_1) = \hat{N}\hat{p}$$

and

$$\hat{E}(u_j) = \hat{N}(1 - \hat{p})^{j-1}\hat{p}, \qquad \text{for } j > 1 \ ,$$

where $\hat{N}$ and $\hat{p}$ are the ML estimates of N and p. From Fig. 4.2, $\hat{N} = 621$ and $\hat{p} = 0.414$. (Three-digit accuracy is sufficient for these computations.) For this example,

$$\hat{E}(u_1) = 621 \times 0.414 = 257.1,$$

$$\hat{E}(u_2) = 621 \times (1 - 0.414) \times 0.414 = 150.7,$$

$$\hat{E}(u_3) = 621 \times (1 - 0.414)^2 \times 0.414 = \ \ 88.3,$$

and

$$\hat{E}(u_4) = 621 \times (1 - 0.414)^3 \times 0.414 = \ \ 51.7,$$

The quantity $[u_j - \hat{E}(u_j)]^2/\hat{E}(u_j)$ is then computed for each capture occasion ($j = 1, 2, 3, 4$ in this example). For example, for $j = 1$ we have $(260 - 257.1)^2/257.1 = 0.0327$. For $j = 2, 3,$ and 4 the corresponding results are 0.6244, 0.8572, and 0.0559. The sum of these four values is the goodness of fit test statistic. For this example, the sum is 1.570. The test statistic is printed by CAPTURE, along with other information, as part of the "generalized removal method" discussed below, for reasons related to the overall structure and logic of program CAPTURE.

If the constant capture probability model fits the data perfectly, the test statistic value will be zero. The poorer the fit of the model to the data, the larger the test statistic value. To judge the fit or lack of fit, we need to know the probability that the test statistic value will be as large as, or larger than, the observed value (such as 1.570) given that the constant capture probability model is true. This observed "significance level" is computed by program CAPTURE (see Fig. 2.9). In the example given above from Fig. 4.2, the probability of an observed test statistic value exceeding 1.570 is 0.4567. Thus, this test statistic is not unusually large, and we conclude that the model adequately fits the data. For philosophical reasons, we do not conclude that the model is a true representation of the real world underlying this study, only that the model fits the data.

Another Simulation Example

To illustrate the sampling variability of data and parameter estimates under even this simple, constant capture probability model, we generated 10 independent replications for the situation $N = 200$, $p = 0.20$, and $t = 5$. Table 4.3 shows the actual captures, the resultant ML estimates of N and p, and the (approximate) 95% confidence interval limits.

Table 4.3 shows that the estimates of N are quite variable (as are the actual removals from replicate to replicate): $\hat{N}$ ranges from 169 to 249. The average $\hat{N}$ from these 10 replications is 206, which is close to the true value of $N = 200$. Of the 10 confidence intervals, only the one for replicate 9 does not cover the true value of N. These results illustrate the variable nature of the data and estimators, even when the underlying model is known to be true.

TABLE 4.3. Results of 10 independent replications of the constant capture probability removal model with $N = 200$, $p = 0.20$, and $t = 5$. Notice that $\hat{N}$ varies from 169 to 249; this sampling variation is to be expected under this model. Notice also that all the confidence intervals except replicate 9 cover the true value of N.

Replicate	u_1	u_2	u_3	u_4	u_5	$\hat{N}(\hat{se}(\hat{N}))$	$\hat{p}$	95% Confidence Interval Limits	
1	37	36	31	15	18	200(30.7)	0.205	139	261
2	38	29	31	22	20	249(61.1)	0.152	129	369
3	43	33	30	20	18	209(30.6)	0.208	149	269
4	33	29	34	18	16	215(46.2)	0.169	124	306
5	48	34	25	21	22	219(31.9)	0.206	156	282
6	45	36	28	19	16	191(20.2)	0.243	149	233
7	37	25	32	23	14	209(41.4)	0.178	127	291
8	42	25	31	19	20	220(42.9)	0.177	135	305
9	55	30	29	15	15	179(12.6)	0.300	154	204
10	39	26	27	14	16	169(23.0)	0.225	123	215
Averages	41.7	30.3	29.8	18.6	17.5	206.0	0.206	137.9	272.9

In practice there is only one repetition. It is important to recognize that innate sampling variability will occur and that the results of any study are just one of many possible outcomes. Thus the computed estimate $\hat{N}$ cannot be expected to equal the true N. The sampling variability of $\hat{N}$ must be recognized and estimated. Moreover, it is also important to present a confidence interval on N that will express a likely range of values for the true population size.

There is another point to be made. In this example, we used a capture probability of 0.2. This value is at the low end of the scale of acceptable capture probabilities required to get precise and unbiased population estimates from removal studies. The larger the capture probability, the more precise will be $\hat{N}$; that is, the lower will be the sampling variability. We recommend $p \geq 0.4$ for really good results in the typical removal study, having N of a few hundred and $t = 3$ to 6.

Failure of Removal Experiments

The basis for estimating population size in removal experiments is that the population size is reduced significantly on each sampling occasion. The number of animals caught should tend to diminish: $u_1 > u_2 > u_3$, and so on. If no depletion is realized, the experiment is said to "fail"; that is, unless the number caught tends to decrease, the model parameters cannot be estimated. *Seber and Whale (1970)* showed that N and p can be estimated from data when the following "failure criterion" is satisfied:

$$\sum_{j=1}^{t} (t + 1 - 2j)u_j > 0 \ .$$

If the criterion is just barely satisfied, the point estimators and their sampling variance will have very poor properties. Failure of removal experiments can be avoided by conducting the sampling so that p is as large as possible.

Generalized Removal Method

The Basic Idea. The constant capture probability model does not always fit removal data. An example from *Otis et al. (1978:46-48)* illustrates the problem. The removal data, given in Fig. 4.3, are from *Andrezejewski and Jezierski (1966).* They were estimating population densities of the European hare by using drive trapping. From Fig. 4.3 we see that $u_1 = 722$, then u_2 drops off sharply to 191. After that, the drop-off in removals is much less severe. The pattern suggests that the constant capture probability model does not fit these data. The chi-square goodness of fit test confirms this suspicion; from Fig. 4.3 the goodness of fit test value for the constant capture probability model is 13.150, with a significance level of 0.0014. This significance level means that there is only a probability of 0.0014 that a chi-square test statistic value this large, or larger, would result if in fact the constant capture probability model were the true model for these data. Therefore, we are justified in rejecting this model and concluding that it is not valid for these data.

Having rejected the constant capture probability model as providing a good fit, we must either base the estimate of population size on a different model or accept the estimate from a model that does not fit. Sometimes the point estimate of N is useful, even when the model does not fit, but we should never feel comfortable in those circumstances. The sampling variance will be poor and usually will be underestimated.

If the constant capture probability model does not fit, we must generalize it—that is, make it more flexible by allowing some degree of unequal capture probabilities. The most general removal model would allow a different (average) capture probability to apply to the uncaught animals still in the population on each capture occasion. Such a model would have $t + 1$ parameters: N = population size and p_j = capture probability applicable to the $N - (u_1 + \ldots + u_{j-1})$ remaining individuals at the start of occasion j for $j = 1$ to t. However, with only t pieces of data $(u_1, \ldots, u_t)$ we cannot estimate $t + 1$ parameters. This model is too general to be of any use. Some reduction in the number of parameters is necessary—for example, by assuming a relation between the capture probabilities $p_1, \ldots, p_t$. The constant capture probability model assumes $p_1 = p_2 = \ldots = p_t = p$.

The two possible generic sources of variation in the capture probabilities $p_1, \ldots, p_t$ are variation associated with time (or capture occasion) and variation intrinsic in the capture probabilities of individuals. The latter source we call "heterogeneity" (Chapter 1). Both types have been discussed with reference to capture-recapture studies (Chapter 3). Note that in a removal study, there can be no behavioral variation in capture probabilities of the type defined and discussed in Chapter 3. If the capture probabilities vary because of heterogeneity, a generalized removal model is possible; however, we know of no way to deal with time variation in a removal study. Therefore, we must conduct the study so as to minimize any time variation in capture probabilities. In electrofishing studies, a standardized method

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OCCASION          J=     1    2    3    4
TOTAL CAUGHT   M(J)=     0  722  913  982 1018
NEWLY CAUGHT   U(J)=   722  191   69   36

  K      N-HAT      SE(N)        CHI-SQ.    PROB.     ESTIMATED P-BAR(J),J=1,..., 4

  1     1028.21  3.789703        13.150    0.0014     0.6806  0.6806  0.6806  0.6806
  2     1039.10  7.658751         1.528    0.2164     0.6948  0.5916  0.5916  0.5916

POPULATION ESTIMATE IS        1039 WITH STANDARD ERROR      7.6588

APPROXIMATE 95 PERCENT CONFIDENCE INTERVAL        1023 TO        1055
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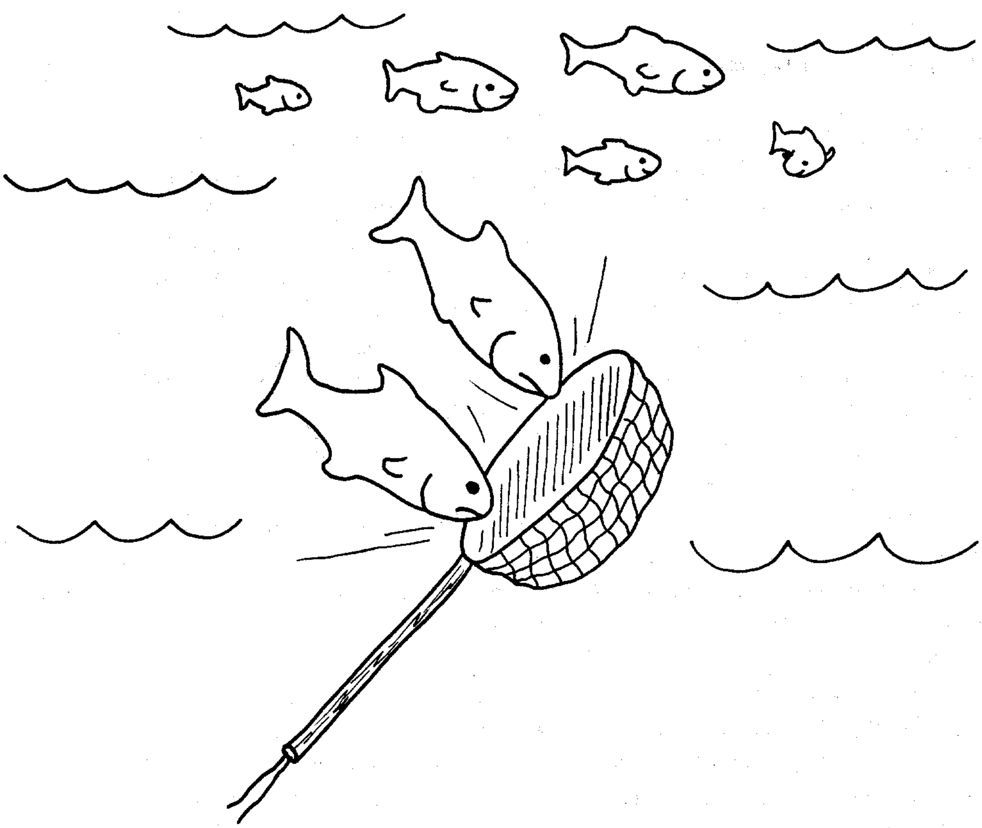
Fig. 4.3. Removal data on hares from Andrezejewski and Jezierski (1966). The data are from an actual field study with four removal occasions; true N is not known. The generalized removal estimator has been applied. For $k = 1$ removal occasions, the model is the constant capture probability model. In the generalized removal method, k represents the number of different capture probability parameters in the model.



In electrofishing, larger fish have greater capture probabilities.

must be used on each occasion. In small-mammal trapping, the method must be standardized and trapping must be done during constant environmental conditions.

Intrinsic variation in capture probabilities has been demonstrated for electrofishing by *Cross and Scott (1975)* and *Bohlin and Sundstrom (1977)*. This means that capture probabilities vary even within size or age classes of fish. Intrinsic variation also is well documented in trapping studies of small mammals.

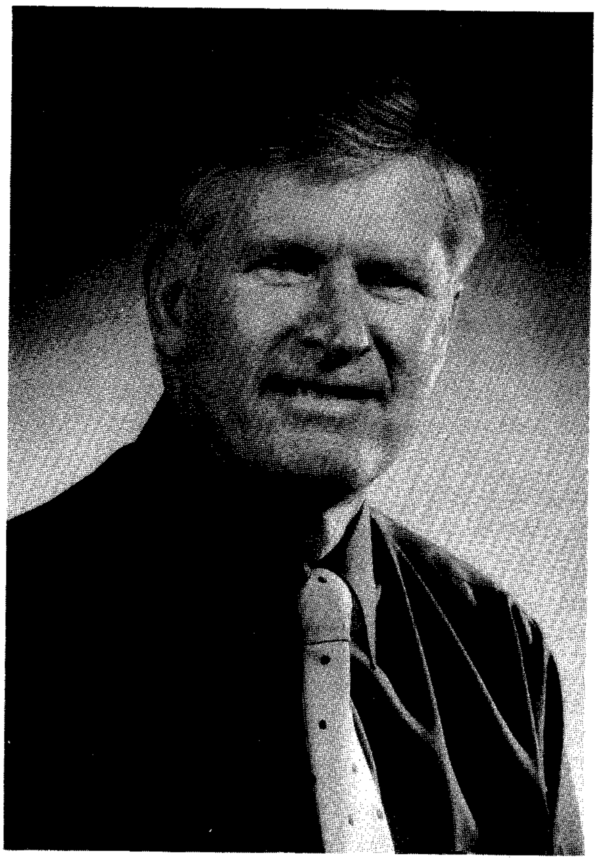
As an extreme, hypothetical example of heterogeneity, imagine a population of 200 in which 50 individuals have a capture probability of 1.0, and 150 individuals have a capture probability of 0.5. On the first occasion, all 50 individuals with a capture probability of 1.0 will be caught, that is, removed. Also, on the average, 75 of the 150 individuals with a capture probability of 0.5 will be caught, leaving 75 individuals each with a capture probability of 0.5. Thus, on and after occasion 2, the constant capture probability model becomes valid. But on the first occasion the average capture probability for the population is 0.625 [$=(1 \times 50 + 0.5 \times 150)/200$]. If the constant capture probability model is applied to removal data from such a population, N will be underestimated. (Numerous empirical studies of the removal method on ponds and small lakes have shown that N usually is underestimated.)

If heterogeneity is present, there is a tendency for the individuals with higher capture probabilities to be caught before the individuals with lower capture probabilities. This tendency causes a decrease in successive capture probabilities. Thus, we expect that $p_1 > p_2 > p_3 > \ldots > p_t$. In the above extreme example, $p_1 = 0.6250$, but $p_2 = p_3 = \ldots = p_t = 0.5$. A less extreme example is a population size of 200, composed of four 50-member subpopulations, with the respective capture probabilities 0.8, 0.6, 0.4, and 0.2. For five removal occasions, we would have $p_1 = 0.5000$, $p_2 = 0.4000$, $p_3 = 0.3333$, $p_4 = 0.2920$, and $p_5 = 0.2655$. This example illustrates the expected sequence of removal probabilities applicable to each occasion under the assumption of heterogeneity within the population. The p_j's decrease, but tend to level off. Thus, although the difference between p_1 and p_2 is 0.1, the difference between p_4 and p_5 is only 0.0265. In the absence of specific information about the values of these capture probabilities, a logical modeling approach is to allow the first few p_j's to differ, but thereafter to assume that $p_{j+1} = p_{j+2} = \ldots = p_t$. In so doing, we seek only an adequate fit to the data, not a perfect model, and we make no assumptions about how the p_j's decrease.

Examples of the Generalized Removal Model. *Otis et al. (1978:44-50)* presented a generalized removal method that implements the ideas presented here (see also *Skalski and Robson 1979*). The method involves fitting successively more general removal models, starting with the constant capture probability model, until an adequate fit to the data is found. (The method has some similarities to step-wise regression.) The second model of the sequence allows the capture probability for the first capture occasion to differ from the capture probabilities on the second and subsequent occasions. Thus, the parameters for the second model are N, p_1, and p ($= p_2 = \ldots = p_t$). Specifically, this model has two capture probability parameters.

The results of the second model are presented in Fig. 4.3 in the $k = 2$ row, and the results for the constant capture probability model are presented in the $k = 1$ row. (The value of k is the number of different capture probability parameters in the model.) For $k = 1$, the constant capture probability model does not fit ($P = 0.0014$), but for $k = 2$ the chi-square goodness of fit statistic is 1.528, with $P = 0.2164$. We judge that the second model fits these data adequately, and hence we use it as the basis for estimating N. Consequently, we take $\hat{N} = 1039$, with a standard error of 7.66 and a confidence interval of 1023 to 1055.

The estimator of N used with this generalized removal model ($k = 2$ in the above example) is the ML estimator. Details of its theory and computation are found in *Otis et al. (1978:40-43,45-50, 112-114).*



Douglas S. Robson

Douglas Robson has been interested in capture-recapture and removal sampling since the early 1950s and has published more than 20 papers on many aspects in this area. Born in North Dakota, he took a B.S. degree in statistics from Iowa State University, received M.S. and Ph.D. degrees from Cornell University in statistics, and has had professional experience at the University of Washington, Princeton University, and Colorado State University. He has been Professor of Biological Statistics at Cornell since 1963.

Robson's contributions to capture-recapture have ranged from fairly theoretical to very applied work, for example, sample size estimation. His most recent interests lie in the estimation of survival rates in open-population models and in removal experiments. Robson certainly has been one of the leading contributors to the development of testing and estimation techniques in capture-type studies. He has worked with a host of other people contributing to the general theory, including C. Brownie, D. G. Chapman, R. M. Cormack, G. J. Paulik, K. H. Pollock, and H. A. Reiger. (Recent photograph.)

Larger mammals can be captured in wire live traps such as the one shown. (Photograph courtesy of Raymond Greenwood and Alan Sargeant.)

Two types of traps can be used at the same station to catch small mouse-sized mammals (left trap), and larger chipmunk-sized mammals (right trap). (Photograph courtesy of Robert Streeter.)

The basic assumption behind this generalized removal model is that of heterogeneity of capture probabilities in the sampled population. This should result in p_2 being less than p_1. Program CAPTURE prints the ML estimator of the distinct capture probabilities in each generalized removal model. From Fig. 4.3 for row $k = 1$, there is only one distinct capture probability, thus $\hat{p}_1 = \hat{p}_2 = \hat{p}_3 = \hat{p}_4 = \hat{p} = 0.6806$. However, for the next more general model (on row $k = 2$), $\hat{p}_1 = 0.6948$ and $\hat{p}_2 = \hat{p}_3 = \hat{p}_4 = \hat{p} = 0.5916$. Thus, after the first capture occasion the estimated average capture probability of hares still uncaught is 0.6, rather than 0.7. We interpret this change to be a result of an innate heterogeneity existing in the population and the tendency for more catchable animals to be caught first.

To demonstrate the generalized removal method further, we present more real data, this time from the use of removal sampling to estimate stream bottom benthos (see *Carle 1976; Carle and Strube 1978).* Figure 4.4 presents the numbers of Ephemerellidae found in five removals from one site on the Cache la Poudre River in Colorado;* the field methodology was essentially that of *Carle (1976).* Just a look at the removal data (310, 26, 14, 7, 6) shows that the constant capture probability model does not fit. Indeed, the goodness of fit test to that model has a chi-square test statistic value of 77.118; taken to four decimal places, the probability of a value this large, if the constant probability model is true, is 0.0000. In Fig. 4.4, rows $k = 2$ and $k = 3$ show the results of fitting the two- and three-parameter generalized removal models. The two point estimators of N hardly differ because apparently almost all individuals were caught.

From Fig. 4.4, we see that the model with two capture parameters ($k = 2$) provides an adequate fit to these data. For that model, $\hat{N} = 368$, with a standard error of 4.2. Perhaps more interesting are the estimates of capture probabilities. For the two-parameter model, $\hat{p}_1 = 0.8425$ and the subsequent estimated capture probabilities are $\hat{p} = 0.4460$. The drop in capture probabilities is dramatic. It is consistent with a model in which the capture probabilities are fairly high for most individuals, but are moderate to low for a few individuals.

The generalized removal model with three parameters also fits the data of Fig. 4.4 (row $k = 3$), as it should if the less general model with two parameters fits. In this model, the three capture probabilities are p_1, p_2, and $p_3 = p_4 = p_5 = p$. We see that $\hat{p}_1 = 0.8418$ is almost the same as $\hat{p}_1 = 0.8425$ for the two-parameter model. Also, $\hat{p}_2 = 0.4464$ and $\hat{p}_3 = \hat{p}_4 = \hat{p}_5 = \hat{p} = 0.4375$ are only slightly different from the

*This information was provided by R. F. Raleigh, US Fish and Wildlife Service, Ft. Collins, CO 80526.

```
OCCASION            J=     1    2    3    4    5
TOTAL CAUGHT     M(J)=     0  310  336  350  357  363
NEWLY CAUGHT     U(J)=   310   26   14    7    6

   K       N-HAT       SE(N)        CHI-SQ.      PROB.      ESTIMATED P-BAR(J),J=1,...., 5

   1     363.00 0.4118716           77.118      0.0000      0.7857  0.7857  0.7857  0.7857  0.7857
   2     367.96 4.208916             0.703      0.7035      0.8425  0.4460  0.4460  0.4460  0.4460
   3     368.24 6.008948             0.640      0.4237      0.8418  0.4464  0.4375  0.4375  0.4375


POPULATION ESTIMATE IS              368 WITH STANDARD ERROR          4.2089

APPROXIMATE 95 PERCENT CONFIDENCE INTERVAL            359 TO          377
```

Fig. 4.4. Removal data on stream bottom benthos, Ephemerellidae, from one site on the Cache la Poudre River, Colorado. The circular depletion sampler described in Carle (1976) and Carle and Strube (1978) was used to obtain these data.

```
OCCASION           J=     1    2
TOTAL CAUGHT    M(J)=     0  310  336
NEWLY CAUGHT    U(J)=   310   26

ESTIMATED PROBABILITY OF CAPTURE, P-HAT =     0.919746


POPULATION ESTIMATE IS          338 WITH STANDARD ERROR        1.7377

APPROXIMATE 95 PERCENT CONFIDENCE INTERVALS         334 TO          342
```

Fig. 4.5. Application of the removal estimator to only the first two occasions of the stream bottom benthos data shown in Fig. 4.4. Of necessity, the constant capture probability model is used here. The results are misleading; compare them with those in Fig. 4.4 for the entire data set ($t = 5$).

two-parameter model values. Again, the result is consistent with the adequacy of the two-parameter model for these data.

What if only two capture occasions had been used for the example in Fig. 4.4? The results would be those shown in Fig. 4.5. First, because no goodness of fit test is possible, we have no clue that the constant capture probability model does not fit. The estimated capture probability of 0.92 is not only grossly in error, but is also misleading, because it suggests that virtually all individuals have been caught after two removals. The estimate of N is 338, with an estimated approximate 95% confidence interval of 336 to 342. Remember that if the computed lower limit is less than the total number of individuals seen, the lower limit should be replaced by the number of individuals actually seen. In fact, at least 363 organisms were present; thus the estimate of 338 is clearly too small. More than two removals are required to detect such problems as these.

Such comparisons are also interesting for the data on hares presented in Fig. 4.3. Figure 4.6 presents the results of analyzing only the first two removals of the *Andrezejewksi and Jezierski (1966)* data. Again, there is no clue that the point estimate of $\hat{N} = 980$ is biased low. The computed confidence interval has an upper limit of 1009, which is less than the 1010 hares removed on four occasions.

Finally, we return to the simulated data first given in Table 4.2. Applying the generalized removal method to these data, we get the results shown in Fig. 4.7. As discussed above, this goodness of fit test shows that the model fits, so $\hat{N}$ is taken as 621. Note that for the model in which p_1 is allowed to differ from $p_2 = p_3 = p_4 = p$, we get $\hat{p}_1 = 0.4132$ and $\hat{p} = 0.3952$, which is to be expected because all p_j are the same (0.4).

An Example Using Fish Removal Data. The constant capture probability model does not fit all fish removal data. Figure 4.8 is an example of data from a major study of the removal method applied to fish in small streams *(Mahon 1980)*. Mahon conducted more than a dozen removal experiments; he obtained well over 100 data sets, with the data partitioned by fish species and size. After each experiment, consisting of 4 to 8 removal occasions, he collected the fish remaining in the stream segment by using rotenone. Thus, he knew the true population sizes. We illustrate the generalized removal method for fish

```
OCCASION          J=     1    2
TOTAL CAUGHT    M(J)=    0  722  913
NEWLY CAUGHT    U(J)=  722  191

ESTIMATED PROBABILITY OF CAPTURE, P-HAT =   0.737208


POPULATION ESTIMATE IS          980 WITH STANDARD ERROR       14.6068

APPROXIMATE 95 PERCENT CONFIDENCE INTERVALS           951  TO          1009
```

Fig. 4.6. Application of the removal estimator to only the first two removal occasions of the Andrezejewski and Jezierski (1966) study shown in Fig. 4.3. Of necessity, the constant capture probability model is used here. The results are again misleading; compare them with those in Fig. 4.3.

```
OCCASION           J=     1    2    3    4
TOTAL CAUGHT     M(J)=    0  260  401  498  548
NEWLY CAUGHT     U(J)=  260  141   97   50

  K       N-HAT     SE(N)          CHI-SQ.     PROB.       ESTIMATED P-BAR(J),J=1,...., 4

  1      620.98  16.94006           1.568     0.4567       0.4136  0.4136  0.4136  0.4136
  2      629.28  26.25738           1.246     0.2643       0.4132  0.3952  0.3952  0.3952


POPULATION ESTIMATE IS          621 WITH STANDARD ERROR      16.9401

APPROXIMATE 95 PERCENT CONFIDENCE INTERVAL           587  TO         655
```

Fig. 4.7. Results of applying the generalized removal method to the simulated data given in Table 4.2. With four removal occasions, the first two removal models are fitted to the data; $k = 1$ is the constant capture probability model. For $k = 2$, p_1 is allowed to be different from $p_2 = p_3 = p_4 = p$. Because the constant capture probability model fits the data, the results, $\hat{p}_1 = 0.4132$ and $\hat{p} = 0.3952$ for $k = 2$ are very close both to each other and to the true value, $p = 0.4$. Compare these results with those in Fig. 4.2.

with data from one of Mahon's study stations. The data are for fantail darter (*Etheostoma flabellare*) longer than 35 mm. The true population size for individuals of this species and size was $N = 1151$.

Figure 4.8 shows the removals for the seven sampling occasions ($t = 7$) used at this station. The 666 fantail darters caught were only 58% of the true population. We see from the figure that the constant capture probability model produced an estimate of $\hat{N} = 900(\pm 48)$. The chi-square goodness of fit test statistic for this model was 9.071, which has an observed significance level of $P = 0.106$. We reject a removal model, for lack of fit, if this observed significance level is less than 0.20 because we believe it is better to sacrifice some precision to minimize bias. This example illustrates such a tradeoff. The generalized removal model with $k = 2$ produces $\hat{N} = 1025$, with an estimated standard error of 105. The (approximate) 95% confidence interval on N is 819 to 1231; it covers N (= 1151). By contrast, for $k = 1$ (the constant capture probability model), the interval of 805 to 995 does not come close to covering the true value of N.

Regression, or Catch Per Unit Effort Methods

The wildlife and fisheries literature presents several methods for estimation of N based on the constant capture probability removal model. These methods are of two types: (1) regression methods or (2) the maximum likelihood method and its modifications or approximations (see *Zippin 1956; Carle and Strube 1978).* The regression methods often are referred to as methods based on "catch per unit effort" (CPUE). This acronym derives from the fisheries literature, especially concerning commercial fisheries, where fishing provides catch statistics but where units of fishing effort vary in each time period. In wildlife studies, effort usually can be nearly equal on each capture occasion. In removal trapping, keeping the same number of traps working on each occasion is considered to provide equal effort. In electrofishing, standardization of the technique provides equal effort. We do not deal here with CPUE methods for varying effort on each occasion, but both *Ricker (1975)* and *Seber (1982)* give an introduction to the methodology.

```
OCCASION            J=     1    2    3    4    5    6    7
TOTAL CAUGHT     M(J)=     0  180  295  389  473  548  606  666
NEWLY CAUGHT     U(J)=   180  115   94   84   75   58   60

   K      N-HAT      SE(N)        CHI-SQ.    PROB.     ESTIMATED P-BAR(J),J=1,...., 7

   1     900.40   48.45878         9.071    0.1063     0.1747  0.1747  0.1747  0.1747  0.1747  0.1747  0.1747
   2    1025.39   104.7211         1.146    0.8869     0.1755  0.1327  0.1327  0.1327  0.1327  0.1327  0.1327
   3    1062.05   154.9901         0.909    0.8234     0.1695  0.1304  0.1237  0.1237  0.1237  0.1237  0.1237
   4    1041.35   194.3479         0.922    0.6308     0.1729  0.1335  0.1259  0.1289  0.1289  0.1289  0.1289
   5    1038.21   292.5283         0.927    0.3357     0.1734  0.1340  0.1265  0.1294  0.1297  0.1297  0.1297


POPULATION ESTIMATE IS         1025 WITH STANDARD ERROR    104.7211

APPROXIMATE 95 PERCENT CONFIDENCE INTERVAL         819 TO        1231


HISTOGRAM OF U(J)


FREQUENCY     180  115   94   84   75   58   60
------------------------------------------------
EACH * EQUALS    18 POINTS

      180       *
      162       *
      144       *
      126       *
      108       *    *
       90       *    *    *    *
       72       *    *    *    *    *
       54       *    *    *    *    *    *    *
       36       *    *    *    *    *    *    *
       18       *    *    *    *    *    *    *
------------------------------------------------
```

Fig. 4.8. Results of applying the generalized removal method to data on fantail darters longer than 35 mm (from Mahon 1980). The true value of $N = 1151$ was known because after the seven removals, rotenone was used to collect the remaining fish.

Under the model of constant capture probability, all regression-based CPUE methods are inferior to the ML estimation method. We will discuss one regression-based method primarily because it appears so frequently in the literature. First, however, we must define another symbol in addition to u_j: M_j = the number of individuals marked and hence removed from the population before the j^{th} capture occasion. Thus $M_1 = 0$, because before the first capture occasion no individuals have been marked and removed from the population. Before the second capture occasion u_1 individuals have been marked and removed, hence $M_2 = u_1$. After the second capture occasion, $u_1 + u_2$ individuals have been marked and removed, so that $M_3 = u_1 + u_2$. In general, $M_j = u_1 + \ldots + u_{j-1}$. Also defined (but not used in the regression method) is $M_{t+1} = u_1 + u_2 + \ldots + u_t$, which is the total number of individuals marked and removed and hence known to be in the population. Any admissible estimator of N must be at least as large as M_{t+1}.

Under the constant capture probability model, a linear structural relation between the two variables $E(u_j)$ and $E(M_j)$ is, specifically,

$$E(u_j) = pN - pE(M_j) \tag{4.2}$$

or, equivalently,

$$E(M_j) = N - \left(\frac{1}{p}\right) E(u_j) \ . \tag{4.3}$$

Based on Eq. (4.2), *Hayne (1949a)* published the following regression method of estimating N: regress u_j on M_j, $j = 1, \ldots, t$, to get an estimate of p (as the slope of the regression equation) and an estimate of $-pN$ (the intercept of the regression equation). Symbolically, the fitted regression is

$$u_j = \hat{a} + \hat{b}\, M_j, \qquad j = 1, \ldots, t, \tag{4.4}$$

where $\hat{a} = \widehat{pN}$ and $\hat{b} = -\hat{p}$, so that

$$\frac{\hat{a}}{-\hat{b}} = \frac{\widehat{pN}}{-(-\hat{p})}$$

$$= \hat{N} \,. \tag{4.5}$$

Basing the regression on Eq. (4.3) rather than on Eq. (4.4) has statistical (theoretical) advantages, but commonly it has been based on the form of Eqs. (4.2) and (4.4) in conjunction with a plot of the data as u_j (on the y-axis) versus M_j (on the x-axis). In such a plot, the point where the line intercepts the x-axis is the estimate of N, the mathematical equivalent to Eq. (4.5).

From Fig. 4.2 we have the pair of variables u_j and M_j, as

j	u_j	M_j
1	260	0
2	141	260
3	97	401
4	50	498

A plot of these data and the results of applying the simple linear regression of u_j on M_j, using Eq. (4.4), are shown in Fig. 4.9; $\hat{a}$ and $\hat{b}$ are explained above, and r is the correlation coefficient of u_j and M_j. From this regression, the estimate of p is $\hat{p} = -\hat{b} = 0.41488$ and the estimate of N is $\hat{N} = (257.2/0.42488) = 620$. Note also that $M = 620$ is the intercept of the line with the x-axis.

These point estimates of N and p compare well with the ML estimates in Fig. 4.2. However, it is very difficult to obtain a valid estimate of the sampling variance of this regression estimator of N. Even if we could obtain a valid variance estimate, statistical theory assures us that the ML estimate of N has a smaller sampling variance under the assumed model and hence is the better estimator.

The usual model for simple linear regression (for a sample size of n pairs of variables y_j, x_j) is, symbolically,

$$y_j = a + bx_j + \varepsilon_j, \qquad j = 1, \ldots, n,$$

under the assumption that the n pairs of variables (y_j, x_j) are independent of each other. An alternative expression of this is that the "errors" $\varepsilon_1, \ldots, \varepsilon_n$ are assumed to be independent. Moreover, it is assumed that the sampling variance of ε_j is a constant, say σ^2, for all $j = 1, \ldots, n$.

These usual assumptions of simple linear regression are violated severely by the application in Eq. (4.4). Specifically, the different pairs of the variables (u_j, M_j) are highly correlated, so that the assumption of independence of the errors is violated. Also, the sampling variances of the errors are not equal; instead, they are proportional to u_j. Consequently, the usual formulas for the sampling variances of $\hat{a}$ and $\hat{b}$ are invalid.

For the simulated data that fit the constant capture probability model, the correlation of M_j and u_j is $r = -0.99761$. Applied to the hare data of *Andrezejewski and Jezierski (1966)*, this same regression method produces $r = -0.99926$, which is a stronger correlation (Fig. 4.10). Yet we know from the results in Fig. 4.3 that the hare data do not fit the constant capture probability model. The disparity demonstrates that the correlation coefficient is useless as a measure of how well this model fits the data. Similarly, visual examination of the plotted data, as in Figs. 4.9 and 4.10, does not serve as a goodness of fit test of the model to the data. Only the chi-square goodness of fit test provides an adequate test of the model fit.

The regression method can, and often does, produce estimates of N below the total numbers of animals caught. For example, when we applied the regression method to the hare data of Fig. 4.3 (Fig. 4.10), we

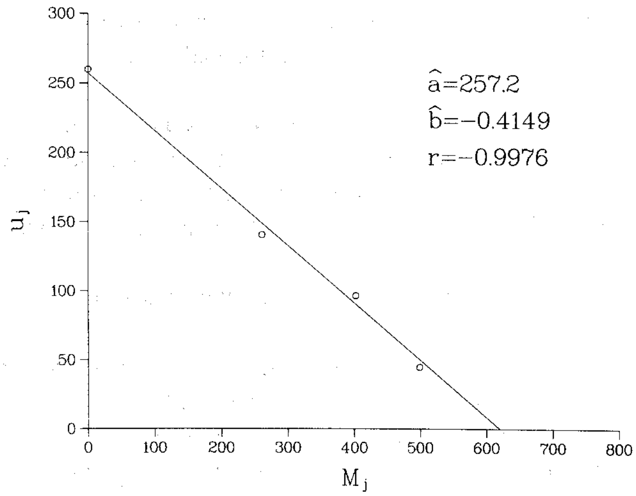


Fig. 4.9. A plot of the u_j, M_j data shown in Table 4.2 and used in Fig. 4.2. The fitted regression line, Eq. (4.4), also is shown. Notice that the intercept of the line and the x-axis is $\hat{N} = 620$.

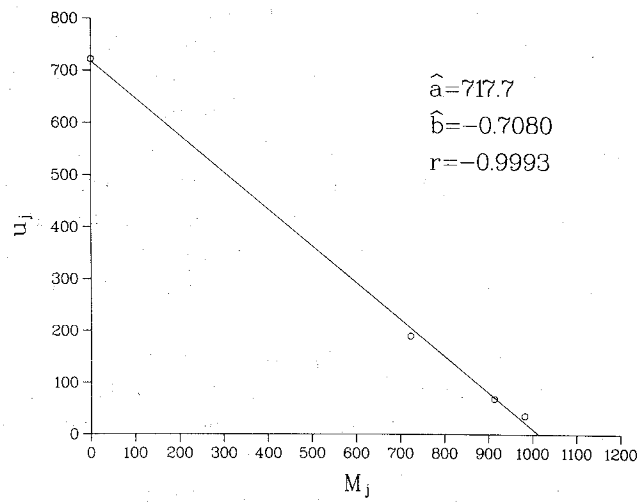


Fig. 4.10. The regression estimator applied to the hare data of Andrezejewski and Jezierski (1966). The correlation is very high, r = −0.99926, and the plotted data apparently are linear, yet these removal data do not fit the constant capture probability model. (See Fig. 4.3.)

obtained $\hat{N} = 717.7/0.70830 = 1014$, even though the total number of hares caught was 1018. Of course, such an estimate is ridiculous. The problem is not hypothetical. *Andrezejewski and Jeziewski (1966)* used exactly this regression method and reported in their paper the point estimate of 1010. They got this number rather than 1014 by rounding the slope estimate to 0.71, computing $\hat{N} = 717.7/0.71$, and truncating the result to 1010. Their variance estimate is also quite invalid; they estimated $\hat{se}(\hat{N}) = 38$.

In contrast, the generalized removal method applied to the hare data of Fig. 4.3 produced $\hat{N} = 1039$ with $\hat{se}(\hat{N}) = 7.7$. Thus, an approximate 95% confidence interval N is 1023 to 1055.

Summary

1. In true removal sampling, each animal is caught only once. The most common applications are snap trapping of small mammals and electrofishing in small streams. In snap trapping the animals are killed. In electrofishing the captured fish usually are held in buckets until the removal passes have been completed, and then the fish are returned to the stream.

2. The assumption of closure is critical to the results of a removal study. If closure is violated, the estimate of (original) population size will be biased—often badly so. If closure fails drastically, the study

becomes a total waste of time and money. If animals leave the study area between capture occasions, the population size N will be underestimated. If they enter the area, N will be overestimated—possibly badly so.

3. Removal studies require a minimum of two capture occasions, and even two occasions do not allow a test of the constant capture probability assumption. If all animals have an average capture probability of at least 0.8, two occasions will suffice because failure of constant capture probability will not matter.

4. The common model for analysis of removal data assumes an equal and constant capture probability (p) for all individuals.

5. If the assumption of equal and constant capture probability is to be tested, there must be at least three capture occasions.

6. To obtain useful results with the removal method, capture probabilities should be at least 0.2, and if they are as low as 0.2, even six capture occasions will give only marginally reliable results.

7. The removal method is not suitable for populations exceeding a few thousand individuals.

8. The removal method will fail to give reliable results unless there is an obvious decrease in number of animals caught over the t capture occasions.

9. We recommend use of the ML estimator of N, although it does not exist in closed form. Its sampling variance is smaller than those of other estimators under the constant p or the generalized removal model. In particular, we note that the ML estimator of N will never be less than M_{t+1} (the number of individuals removed). All commonly used regression methods are based on the same assumptions as the ML estimator, and their estimators of N can be less than M_{t+1} even when the assumptions are true.

10. The assumption of constant capture probability can be relaxed to allow for some degree of heterogeneity. The assumption of heterogeneity leads to the generalized removal method, which fits successively more general models to the data until an acceptable fit is found. For example, the first more general model allows one capture probability, p_1, on occasion 1 and different (but equal) capture probabilities on occasions 2, 3, . . ., t. If this generalized model fits the data, it often does so with just two parameters.

11. Common sources of differences in capture probabilities (heterogeneity) are differences by species, sex, or age. In electrofishing, fish size (within wide limits) influences capture probability—smaller fish are less catchable. If the data are sufficient, we recommend partitioning all data by species and sex, and electrofishing data by two or three broad categories of size.

12. Although some degree of heterogeneity can be allowed for, time variation in capture probabilities totally destroys the usefulness of the removal method. No estimator is possible for a removal study with time variation in the capture probabilities, unless the number of capture occasions is extended until all animals are caught.

13. The estimator of N under the generalized removal is the ML method. It does not exist in closed form.

Questions and Exercises

1. Would you accept a removal study with only one (t = 1) capture occasion?
2. What are the potential defects of removal studies with t = 2 occasions?
3. Can you have an open-model removal study?
4. Can you use removal estimation methods on live-trapping data?
5. In general, do capture-recapture studies yield more information about N than removal studies?
6. Would you accept, as a point estimate of N, a value less than M_{t+1}, the total number of animals removed?
7. Why is kill trapping over a long time period likely to give a poor estimate of N?
8. A biologist, asked to estimate the population size of the endangered lion snail, suggests a removal study over five occasions. Assess his proposal.
9. Are the following removal data useful? $u_1 = 100$, $u_2 = 99$, $u_3 = 105$, $u_4 = 98$, and $u_5 = 95$, with t = 5.

10. A snap trap study of small mammals conducted for 4 days gives $u_1 = 68$, $u_2 = 41$, $u_3 = 25$, and $u_4 = 15$.
   a. Describe the X matrix.
   b. Was the study acceptable; that is, do you expect a reasonable estimate of N to result?
   c. Give a rough estimate of N, then if possible, use program CAPTURE to obtain the exact ML estimate.
11. If true population size is $N = 100$ and a three-occasion removal study has the constant capture probability $p = 0.05$, will the results be useful? Compute the expected numbers removed on the study's three occasions.
12. In studies of small populations (N of at most 200), what capture probability should you have to achieve reliable results if $t = 4$?
13. You conduct a removal study, with carefully controlled equal effort, and find $u_1 = 20$, $u_2 = 15$, $u_3 = 8$, $u_4 = 17$, $u_5 = 29$, and $u_6 = 36$. What is happening?
14. You assess your experimental situation and conclude that closure will be violated significantly; you decide to try a removal study anyway. What can be said about $\hat{N}$ as an estimate of N?
15. Let $\bar{p}_j$ be the average capture probability on removal occasion j. What does $\bar{p}_j$ mean? Why do the $\bar{p}_j$ decrease under model M_{bh}?
16. What sources of heterogeneity are likely to be present in electrofishing? In kill trapping?
17. What happens in a removal study if equal effort fails to be true?