Several methods have been developed for population estimation in which the organisms need to be captured only one time. The first set of these were developed for exploited populations from which individuals were removed as a harvest from the population, and they are loosely described as removal methods. These methods were first developed in the 1940s, so that wildlife and fisheries managers could get estimates of the population under harvest. A discussion of removal methods forms the first section of this chapter.

A second set of methods are of much more recent development and are based on the principle of resighting animals that have been marked. They require an individual animal to be captured only once, and then all subsequent "recaptures" are from sighting records only—the individual never has to be physically captured again. These newer methods were developed for animals with radio-collars but can be used with any kind of mark that is visible to a distant observer. We shall discuss these resighting methods in the second section of this chapter.

Mark-recapture methods have developed into very complex statistical methods during the last 10 years. While many of these methods are beyond the scope of this book, we
can still use them for field populations once we understand their assumptions. The third section of this chapter provides an overview of computer-intensive methods that can be used for mark-recapture estimation.

3.1 EXPLOITED POPULATION TECHNIQUES

A special set of techniques has been developed for estimating population size in exploited populations. Many of these techniques are highly specific for exploited fish populations (Ricker 1975; Seber 1982), but some are of general interest because they can be applied to wildlife and fisheries problems as well as other field situations. I will briefly describe two types of approaches to population estimation that can be used with exploited populations.

3.1.1 Change-in-Ratio Methods

The idea that population size could be estimated from field data on the change in sex ratio during a hunting season was first noted by Kelker (1940). When only one sex is hunted, and the sex ratio before and after hunting is known, as well as the total kill, Kelker showed that one could calculate a population estimation from the simple ratio

\[
\left( \text{Fraction of males in population after hunting removals} \right) = \frac{\left( \frac{\text{Number of males before hunting}}{\text{Total population size before hunting season}} \right) - \left( \frac{\text{Number of males removed}}{\text{Total number of animals killed by hunters}} \right)}{\left( \frac{\text{Total population size before hunting season}}{\text{Total number of animals killed by hunters}} \right)}
\]

Several investigators discovered and rediscovered this approach during the last 50 years (Hanson 1963), and only recently has the general theory of change-in-ratio estimators been pulled together (Paulik and Robson 1969; Seber 1982). All change-in-ratio estimators are based on two critical assumptions:

1. The population is composed of two types of organisms, such as males and females, or adults and young.
2. A differential change in the numbers of the two types of organisms occurs during the observation period.

I will use here the general terminology of Paulik and Robson (1969), calling the two types of organisms \(x\)-types and \(y\)-types. To make the situation more concrete, you can think of \(x\)-types as females and \(y\)-types as males.

We define the following symbols:

- \(N_1\) = Total population size at time 1
- \(N_2\) = Total population size at time 2
- \(X_1, X_2\) = Number of \(x\)-type organisms in the population at times 1 and 2
- \(Y_1, Y_2\) = Number of \(y\)-type organisms in the population at times 1 and 2
\[ p_1 = \frac{X_1}{N_1} = \text{Proportion of } x\text{-types in population at time 1} \]
\[ p_2 = \frac{X_2}{N_2} = \text{Proportion of } x\text{-types in population at time 2} \]
\[ R_x = X_2 - X_1 = \text{Net change in numbers of } x\text{-type organisms between times 1 and 2 (may be } + \text{ or } -) \]
\[ R_y = Y_2 - Y_1 = \text{Net change in numbers of } y\text{-type organisms between times 1 and 2 (may be } + \text{ or } -) \]
\[ R = R_x + R_y = \text{Net addition } (+) \text{ to or net removal } (-) \text{ from the total population between times 1 and 2} \]

Given these symbols, we can restate the verbal model of Kelker (1940) given above by the formula:

\[ \hat{N}_1 = \frac{R_x - \hat{p}_2 R}{\hat{p}_2 - \hat{p}_1} \quad (3.1) \]

This is the generalized change-in-ratio estimator of population size. We can illustrate this method with some hypothetical data on ringed-neck pheasants used by Paulik and Robson (1969). During a preseason survey, 800 of 1400 adult birds were females, and after hunting was over, 1800 of 2000 birds were females. The total kill was estimated to be 8000 male pheasants and 500 females. Thus:

\[ \hat{p}_1 = \frac{800}{1400} = 0.571428 \]
\[ \hat{p}_2 = \frac{1800}{2000} = 0.900000 \]
\[ R_x = -500 \]
\[ R_y = -8000 \]
\[ R = R_x + R_y = -8500 \]

Thus, from equation (3.1),

\[ \hat{N}_1 = \frac{-500 - (0.900000)(-8500)}{(0.900000) - (0.571428)} = 21,761 \text{ pheasants} \]

Because of the structure of this formula, it is desirable to keep the estimated proportions to 6 or more decimal places to minimize rounding errors.

It follows that

\[ \hat{N}_1 = \hat{p}_1 \hat{N}_1 \]
\[ = (0.571428)(21,761) = 12,435 \text{ female pheasants at time 1} \]

and

\[ \hat{N}_2 = \hat{N}_1 + R \]
\[ = 21,761 + (-8500) = 13,261 \text{ pheasants alive at time 2} \]
Confidence intervals for this population estimate can be calculated in two different ways, depending on sample size (Paulik and Robson 1969).

**Large samples** When approximately 500 or more individuals are sampled to estimate \( p_1 \) and an equally large number to estimate \( p_2 \), you should use the normal approximation:

\[
\text{Variance}(\hat{N}_1) = \frac{\hat{N}_1^2 [\text{variance}(\hat{p}_1)] + \hat{N}_2^2 [\text{variance}(\hat{p}_2)]}{(\hat{p}_1 - \hat{p}_2)^2}
\]  

(3.2)

where

\[
\text{Variance}(\hat{p}_1) = \frac{\hat{p}_1(1 - \hat{p}_1)}{n_1}
\]  

(3.3)

\[
\text{Variance}(\hat{p}_2) = \frac{\hat{p}_2(1 - \hat{p}_2)}{n_2}
\]  

(3.4)

where \( n_1 = \) Total sample size used to estimate the ratio \( p_1 \) at time 1

\( n_2 = \) Total sample size used to estimate the ratio \( p_2 \) at time 2

This variance formula assumes binomial sampling with replacement and is a reasonable approximation to sampling without replacement when less than 10% of the population is sampled (Seber 1982, 356). It also assumes that \( R_x \) and \( R_y \) (the removals) are known exactly with no error.

For the pheasant example above,

\[
\text{Variance of } \hat{p}_1 = \frac{(0.571428)(1 - 0.571428)}{1400} = 0.0001749
\]

\[
\text{Variance of } \hat{p}_2 = \frac{(0.9)(1 - 0.9)}{2000} = 0.0000045
\]

Thus,

\[
\text{Variance}(\hat{N}_1) = \frac{(21.761)^2(0.0001749) + (13.261)^2(0.0000045)}{(0.428571 - 0.100000)^2}
\]

\[= 840.466\]

The standard error is given by:

\[
\text{Standard error of } \hat{N}_1 = \sqrt{\text{Variance}(\hat{N}_1)}
\]

\[= \sqrt{840.466} = 916.8\]

The 95% confidence limits follow from the normal distribution:

\[
\hat{N}_1 \pm 1.96[\text{S.E.}(\hat{N}_1)]
\]

For these data, we have

\[
21,761 \pm 1.96(916.8)
\]

or 19,964 to 23,558 pheasants.
**Small samples** When less than 100 or 200 individuals are sampled to estimate \( p_1 \) and \( p_2 \), you should use an alternative method suggested by Paulik and Robson (1969). This method obtains a confidence interval for the reciprocal of \( \hat{N}_1 \) as follows:

\[
\text{Variance of } \left( \frac{1}{\hat{N}_1} \right) = \frac{(R_x - \hat{P}_1 R)^2}{(R_x - \hat{P}_2 R)^4} \left( \text{Variance of } \hat{P}_2 \right) + \frac{1}{(R_x - p_2 R)^2} \left( \text{Variance of } \hat{P}_1 \right)
\]  

(3.5)

where

- \( \text{Variance of } p_1 = \) as defined in equation (3.3)
- \( \text{Variance of } \hat{P}_2 = \) as defined in equation (3.4)

and all other terms are as defined above.

This formula assumes that \( R_x \) and \( R_y \) are known without error. If we apply this formula to the pheasant data used above, we have

\[
\text{Variance of } \left( \frac{1}{\hat{N}_1} \right) = \frac{[-500 - (0.571428)(-8500)]^2}{[-500 - (0.90)(-8500)]^4} \times 0.000045
\]

\[+ \frac{1}{[-500 - (0.90)(-8500)]^2} \times 0.0001749\]

\[= 3.7481 \times 10^{-12}\]

**Standard error of \( \left( \frac{1}{\hat{N}_1} \right) \)**

\[= \sqrt{\text{Variance}(1/\hat{N}_1)} \]

\[= \sqrt{3.7481 \times 10^{-12}} = 1.9360 \times 10^{-6}\]

The 95% confidence interval is thus:

\[\frac{1}{\hat{N}_1} \pm 1.96 \left[ \text{S.E.} \left( \frac{1}{\hat{N}_1} \right) \right]\]

\[\frac{1}{21,761} \pm 1.96(1.9360 \times 10^{-6})\]

or \(4.2159 \times 10^{-5}\) to \(4.9748 \times 10^{-5}\)

Inverting these limits to get confidence limits for \( \hat{N}_1 \),

**Lower 95% confidence limit**

\[\frac{1}{4.9748 \times 10^{-5}} = 20,101 \text{ pheasants}\]

**Upper 95% confidence limit**

\[\frac{1}{4.2159 \times 10^{-5}} = 23,720 \text{ pheasants}\]

Note that these confidence limits are asymmetrical about \( \hat{N}_1 \) and are slightly wider than those calculated above using the (more appropriate) large-sample formulas on these data.

The program-group MARK-RECAPTURE (Appendix 2) can do these calculations for the generalized change-in-ratio estimator of population size.

**Planning Change-in-Ratio Studies** If you propose to use the change-in-ratio estimator (equation [3.1]) to estimate population size, you should use the approach outlined by Paulik and Robson (1969) to help plan your experiment. Five variables must be guessed at to do this planning:
1. $\Delta p = p_1 - p_2 =$ Expected change in the proportion of $x$-types during the experiment.
2. $u =$ Rate of exploitation $= R/N_1$, which is the fraction of the whole population that is removed.
3. $f = R_x/R =$ fraction of $x$-types in the removals.
4. Acceptable limits of error for the $\hat{N}_1$ estimate; $\pm 25\%$ might be usual (see page 29).
5. Probability $(1 - \alpha)$ of achieving the acceptable limits of error defined in (4); $90\%$ or $95\%$ might be the usual values here.

Figure 3.1 shows the sample sizes required for *each* sample $(n_1, n_2)$ for combinations of these parameters with the limits of error set at $\pm 25\%$ and $(1 - \alpha)$ as $90\%$. To use Figure 3.1, proceed as follows:

1. Estimate two of the three variables plotted: the change in proportion of $x$-types, the rate of exploitation, and the fraction of $x$-types in the removal.
2. From these two variables, locate your position on the graph in Figure 3.1, and read the nearest contour line to get the sample size required for each sample.

For example, if $60\%$ of the whole population will be harvested and you expect $75\%$ of the harvested animals to be $x$-types, Figure 3.1 shows that sample size should be about 100 for
the first sample and 100 for the second sample (to achieve error limits of ±25% with a 1 − α of 0.90).

Two general points can be noted by inspecting Figure 3.1, and we can formulate them as rules of guidance:

1. Δp, the expected change in proportions, is the critical variable affecting the required sample sizes of change-in-ratio experiments. The rate of exploitation (u) is of minor importance, as is the fraction of x-types in the removals (f).

2. For Δp less than 0.05, this method requires enormous sample sizes and in practice is not useful for field studies. If p is less than 0.10, large sample sizes are needed, and it is especially critical to test all the assumptions of this approach.

Using a series of graphs like that of Figure 3.1, Paulik and Robson (1969) synthesized Figure 3.2, from which one can read directly the required sample sizes for change-in-ratio experiments. We can illustrate the utility of this graph with an example.

Suppose you are planning a change-in-ratio experiment for a deer population and you expect a change in the sex ratio by at least 0.30 over the hunting season. If you desire to estimate population size with an accuracy of ±25%, from Figure 3.2 you can estimate the necessary sample size to be approximately 200–250 deer to be sexed in both the before-hunting sample and the after-hunting sample. If you want ±10% accuracy, you must pay for it by increasing the sample size to 1050–1400 deer in each sample. Clearly, if your budget will allow you to count and sex only 40 deer in each sample, you will get an estimate of N1 accurate only to ±100%. If this is inadequate, you need to reformulate your research goals.

Figures 3.1 and 3.2 are similar in general approach to Figures 2.3 and 2.4, which allow one to estimate samples required in a Petersen-type mark-recapture experiment. Paulik and Robson (1969) show that Petersen-type marking studies can be viewed as a special case of a change-in-ratio estimator in which x-type animals are marked and y-type are unmarked.

All the above methods for change-in-ratio estimation are designed for closed populations and are based on the assumption that all individuals have an equal chance of being sampled in both the first and in the second samples. Seber (1982, Chapter 9) discusses more complex situations for open populations and techniques for testing the assumptions of this method.

If the x-types and the y-types of animals do not have the same probability of being counted, one of the critical assumptions of the change-in-ratio method is violated. Pollock et al. (1985b) have proposed a new procedure for estimating population size when there is unequal catchability. This procedure operates by having two periods of removal in which only x-types are removed in the first period and only y-types in the second period. This occurs in some states, for example, where there is a season for male deer followed by a season for females. The procedure can be diagrammed as follows:

```
\[ t_1 \quad \text{Known removals of} \quad t_2 \quad \text{Known removals of} \quad t_3 \]
\[
\text{Ratio} \quad \text{Ratio} \quad \text{Ratio}
\text{estimated} \quad \text{estimated} \quad \text{estimated}
\]
\[
\text{of} \quad x\text{-types} \quad \text{of} \quad y\text{-types}
\]
Figure 3.2 Sample sizes required for a change-in-ratio estimate of population size at several possible acceptable error limits ($\epsilon$ as a proportion of the population size) with $(1 - \alpha)$ of 0.95. The initial proportion of $x$-types is assumed to be 0.50. Error limits ($\epsilon$) ranging from ±10% of the population size up to ±100% are indicated on the right side of the graph. These estimates are affected only very slightly by changes in the initial proportion of $x$-types between 0.05 and 0.50, and the critical variable is $\Delta p$ (x-axis). The upper limits of the shaded zones are for situations with minimal exploitation, and the lower limits of the shaded zones are for situations with maximal exploitation. By reading sample sizes off the top of the curves, one can operate conservatively. (From: Paulik and Robson 1969.)

Given that you can estimate the proportion of $x$-types in the population at these three times, Pollock et al. (1985b) show how to estimate the initial population size. One advantage of this procedure is that the proportion of $x$-types in the population need not change from time 1 to time 3 (it must obviously change at time 2 if the method is to work!). But the
main advantage of the Pollock design is that it is robust to unequal catchability of the two types of animals. It clearly involves more work however to obtain an estimate of population size.

### 3.1.2 Eberhardt's Removal Method

A simpler use of removal data to estimate population size was suggested by Eberhardt (1982) and has been called the "index-removal" method. If an index of population size (like roadside counts) can be made before and after the removal of a known number of individuals, it is possible to use the indices to estimate absolute density. This method does not require you to classify individuals into x-types and y-types as does the change-in-ratio method, and there is no need to identify individuals. Eberhardt (1982) discusses how this removal method compares with methods based on mark-recapture.

To use Eberhardt's method, an index of population size is obtained before and after the removals. This index is assumed to have some constant but unknown relationship to population size. For example, a roadside count may see 15% of the deer in an area. If you know the number of animals removed from the population after the first index is taken, you can calculate an estimate of population size by the following equation:

\[
\hat{N} = \frac{x_1 R}{x_1 - x_2}
\]  

(3.6)

where  
\(\hat{N}\) = Estimated population size at time 1  
\(x_1\) = Index count at time 1  
\(x_2\) = Index count at time 2  
\(R\) = Number of animals removed

The proportion of animals removed can be estimated from the ratio

\[
\hat{p} = \frac{(x_1 - x_2)}{x_1}
\]

(3.7)

where  
\(\hat{p}\) = Estimated proportion of animals removed

Eberhardt (1982) derives a variance estimate for population size as follows:

\[
s_{\hat{N}}^2 = \left(1 - \frac{\hat{p}}{\hat{p}}\right)^2 \left(\frac{1}{x_1} + \frac{1}{x_2}\right) (\hat{N}^2)
\]

(3.8)

where  
\(s_{\hat{N}}^2\) = Variance of estimated population size

and the other terms are as defined above. From this variance, you can construct the 95\% confidence limits in the usual manner:

\[
\hat{N} \pm 1.96 [\text{S.E.}(\hat{N})]
\]

where  
S.E.\((\hat{N})\) = \(\sqrt{s_{\hat{N}}^2}\) as defined in equation (3.8)

As with mark-recapture estimates, Eberhardt's removal method works best when a high fraction of the population is seen and a high fraction is removed. Table 3.1 gives the expected coefficient of variation of population estimates made by Eberhardt's method. Unless
TABLE 3.1 COEFFICIENTS OF VARIATION OF EBERHARDT’S INDEX REMOVAL POPULATION ESTIMATE FOR VARIOUS VALUES OF THE PROPORTION OF THE POPULATION COUNTED AND THE PROPORTION REMOVED

<table>
<thead>
<tr>
<th>Percentage removed</th>
<th>Proportion seen</th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0.2</td>
<td>0.4</td>
<td>0.6</td>
<td>0.8</td>
<td></td>
</tr>
<tr>
<td>10%</td>
<td>0.92</td>
<td>0.65</td>
<td>0.53</td>
<td>0.46</td>
<td></td>
</tr>
<tr>
<td>20%</td>
<td>0.42</td>
<td>0.30</td>
<td>0.25</td>
<td>0.21</td>
<td></td>
</tr>
<tr>
<td>30%</td>
<td>0.26</td>
<td>0.18</td>
<td>0.15</td>
<td>0.13</td>
<td></td>
</tr>
<tr>
<td>40%</td>
<td>0.17</td>
<td>0.12</td>
<td>0.10</td>
<td>0.09</td>
<td></td>
</tr>
<tr>
<td>50%</td>
<td>0.12</td>
<td>0.09</td>
<td>0.07</td>
<td>0.06</td>
<td></td>
</tr>
<tr>
<td>60%</td>
<td>0.09</td>
<td>0.06</td>
<td>0.05</td>
<td>0.04</td>
<td></td>
</tr>
<tr>
<td>70%</td>
<td>0.06</td>
<td>0.05</td>
<td>0.04</td>
<td>0.03</td>
<td></td>
</tr>
<tr>
<td>80%</td>
<td>0.04</td>
<td>0.03</td>
<td>0.03</td>
<td>0.02</td>
<td></td>
</tr>
</tbody>
</table>

Source: Eberhardt (1982)

the percentage of the population seen is above about 40% and the percentage removed above 20%, the method is not very precise.

Box 3.1 illustrates the use of Eberhardt’s index removal method.

3.1.3 Catch-Effort Methods

In exploited populations it may be possible to estimate population size by the decline in catch-per-unit-effort with time. This possibility was first recognized by Leslie and Davis (1939), who used it to estimate the size of a rat population that was being exterminated by trapping. DeLury (1947) and Ricker (1975) discuss the method in more detail. This method is highly restricted in its use because it will work only if a large enough fraction of the population is removed so that there is a decline in the catch-per-unit-effort. It will not work if the population is large relative to the removals. The following assumptions are also critical for this method:

1. The population is closed.
2. Probability of each individual being caught in a trap is constant throughout the experiment.
3. All individuals have the same probability of being caught in sample i.

The data required for catch-effort models are as follows:

\[ c_i = \text{Catch or number of individuals removed at sample time } i \]
\[ K_i = \text{Accumulated catch from the start up to the beginning of sample time } i \]
\[ f_i = \text{Amount of trapping effort expended in sample time } i \]
\[ F_i = \text{accumulated amount of trapping effort from the start up to the beginning of time } i \]

Table 3.2 gives an example of such data for a fishery operating on blue crabs.
Box 3.1 Eberhardt's Index-Removal Method of Population Estimation

Feral horses were counted before and after a removal program in Oregon with the following results:

\[ x_1 = 301 \text{ horses counted before removals} \]
\[ x_2 = 76 \text{ horses counted after removals} \]
\[ R = 357 \text{ horses removed} \]

Assuming that the visual counts are in direct proportion to population size, we can use equation (3.6) to estimate population size at time 1:

\[ \hat{N} = \frac{x_1 R}{x_1 - x_2} = \frac{301(357)}{301 - 76} = 477.6 \text{ horses} \]

In this example an estimated 63% of the total population were counted in the first index count (301/477.6). The percentage removed is also high (75%). From Table 3.1, the standard error of this population estimate should be about 3–4% of the estimate, so the confidence interval should be approximately ±6–8% of the population size.

The variance of this estimate is, from equation (3.8),

\[ s_{\hat{N}}^2 = \left(1 - \frac{-\hat{p}}{\hat{p}}\right)^2 \left(\frac{1}{x_1} + \frac{1}{x_2}\right)(\hat{N}^2) \]
\[ = \left(1 - 0.74686\right)^2 \left(\frac{1}{301} + \frac{1}{76}\right)(477.6)^2 \]
\[ = 432.566 \]

From this variance we obtain the 95% confidence limits as

\[ \hat{N} \pm 1.96[\text{S.E.}(\hat{N})] \]
\[ 477.6 \pm 1.96[\sqrt{432.566}] \]

or 437 to 518

These confidence limits are ±8.5% of population size.

Eberhardt's removal method is most useful in management situations in which a controlled removal of animals is undertaken and it is not feasible or economic to mark individuals. It must be feasible to count a significant fraction of the whole population to obtain results that have adequate precision.

Under the assumptions listed above, the catch-per-unit-effort is directly proportional to the existing population size. Leslie and Davis (1939) showed that, because the population must be declining from time to time by an amount equal to the catch, a regression plot of:

- x-axis: accumulated catch \((K_i)\)
- y-axis: catch-per-unit-effort \((v_i/f_i)\)
TABLE 3.2  CATCH-EFFORT DATA FOR A POPULATION OF MALE BLUE CRABS
(Calinectes sapidus) FOR A 12-WEEK PERIOD

<table>
<thead>
<tr>
<th>Week no., i</th>
<th>Catch (pounds), $c_i$</th>
<th>Effort (lines per day), $t_i$</th>
<th>Catch per unit effort, $c_i/t_i = Y_i$</th>
<th>Accumulated catch, $K_i$</th>
<th>Accumulated effort, $F_i$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>33,541</td>
<td>194</td>
<td>172.9</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>2</td>
<td>47,326</td>
<td>248</td>
<td>190.8</td>
<td>33,541</td>
<td>194</td>
</tr>
<tr>
<td>3</td>
<td>36,460</td>
<td>243</td>
<td>150.0</td>
<td>80,867</td>
<td>442</td>
</tr>
<tr>
<td>4</td>
<td>33,157</td>
<td>301</td>
<td>110.2</td>
<td>117,327</td>
<td>685</td>
</tr>
<tr>
<td>5</td>
<td>29,207</td>
<td>357</td>
<td>81.8</td>
<td>150,484</td>
<td>986</td>
</tr>
<tr>
<td>6</td>
<td>33,125</td>
<td>352</td>
<td>94.1</td>
<td>179,691</td>
<td>1343</td>
</tr>
<tr>
<td>7</td>
<td>14,191</td>
<td>269</td>
<td>52.8</td>
<td>212,816</td>
<td>1695</td>
</tr>
<tr>
<td>8</td>
<td>9,503</td>
<td>244</td>
<td>38.9</td>
<td>227,007</td>
<td>1964</td>
</tr>
<tr>
<td>9</td>
<td>13,115</td>
<td>256</td>
<td>51.2</td>
<td>236,510</td>
<td>2208</td>
</tr>
<tr>
<td>10</td>
<td>13,663</td>
<td>248</td>
<td>55.1</td>
<td>249,625</td>
<td>2464</td>
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<tr>
<td>11</td>
<td>10,865</td>
<td>234</td>
<td>46.4</td>
<td>263,288</td>
<td>2712</td>
</tr>
<tr>
<td>12</td>
<td>9,887</td>
<td>227</td>
<td>43.6</td>
<td>274,153</td>
<td>2946</td>
</tr>
</tbody>
</table>

Source: Data from Fischler 1965.

should be a straight line. Figure 3.3 illustrates this plot for the blue crab data in Table 3.2. This graph is easy to grasp because the x-intercept (the point where $y = 0$, or the catch-per-unit-effort falls to zero) is the initial population size ($N$), since it represents the exhaustion of the catch. Secondly, the slope of the line is an estimate of the catchability of the individuals, the probability that a given individual will be caught with one unit of effort. With

![Figure 3.3](image-url)  Leslie plot of catch-effort data of Fischler (1965) for a population of male blue crabs. Using the Leslie model, one can estimate initial population size ($N$) by extrapolating the linear regression to the x-axis. In this case (arrow) $N$ is about $330 \times 10^3$ pounds. (Original data in Table 3.2.)
this regression (Figure 3.3) we can estimate these parameters by eye, or to be more precise, use linear regression techniques as follows:

\[
\text{Catchability } \hat{C} = \frac{-\sum_{i=1}^{s} Y_i (K_i - \bar{K})}{\sum_{i=1}^{s} (K_i - \bar{K})^2}
\]  

(3.9)

\[
\text{Population size } \hat{N} = \bar{K} + \left(\frac{\bar{Y}}{\hat{C}}\right)
\]  

(3.10)

where \( Y_i = \text{Catch-per-unit-effort} = c_i/f_i \)

\( \bar{K} = \text{Mean value of } K_i \text{ (accumulated catch)} = \frac{(\Sigma K_i)}{s} \)

\( s = \text{Total number of samples } (i = 1, 2, 3 \ldots s) \)

For example, using the data in Table 3.2,

\[
\bar{Y} = \frac{\Sigma Y_i}{s} = \frac{172.9 + 190.8 + \cdots}{12} = 90.65
\]

\[
\bar{K} = \frac{\Sigma K_i}{s} = \frac{0 + 33,541 + 80,867 + \cdots}{12} = 168,775.75
\]

Thus,

\[
\hat{C} = \frac{-[172.9(0 - 168,775.75) + 190.8(33,541 - 168,775.75) + \cdots]}{[(0 - 168,775.75)^2 + (33,541 - 168,775.75)^2 + \cdots]}
\]

\[= 0.0005614\]

\[\hat{N} = 168,775.75 + \left[\frac{90.65}{(0.0005614)}\right] = 330,268 \text{ pounds}\]

The variance of this population estimate is given by

\[
\text{Variance of } (\hat{N}) = \frac{s_{yx}^2}{C^2}\left[\frac{1}{s} + \frac{(\hat{N} - \bar{K})^2}{\Sigma (K_i - \bar{K})^2}\right]
\]  

(3.11)

where \( s_{yx}^2 = \text{Variance about regression} = \Sigma \frac{[Y_i - \hat{C}(\hat{N} - K_i)]^2}{(s - 2)} \)

as defined in Sokal and Rohlf (1995, 471) and Zar (1996, 327), and \( s = \text{number of samples} \).

When the number of samples is large \((s > 10)\), approximate 95% confidence limits are obtained in the usual way:

\[\text{Standard error of } \hat{N} = \sqrt{\text{Variance of } \hat{N}}\]

\[95\% \text{ confidence limits } = \hat{N} \pm 1.96[S.E.(\hat{N})]\]

When the number of samples is small, use the general method outlined in Seber (1982, 299) to get confidence limits on \( \hat{N} \).

The plot shown in Figure 3.3 provides a rough visual check on the assumptions of this model. If the data do not seem to fit a straight line, or if the variance about the regres-
sion line is not constant, the data violate some or all of the assumptions, and this model is not appropriate. Ricker (1975) discusses how to deal with certain cases in which the assumptions of the model are not fulfilled.

DeLury (1947) and Ricker (1975) provide two alternative models for analyzing catch-effort data based on a semilogarithmic relationship between the log of the catch-per-unit-effort (y-axis) and the accumulated fishing effort ($F_i$) on the x-axis (e.g., Figure 3.4). The calculations are again based on linear regression techniques. For the more general Ricker model, defining $z_i = \log(Y_i)$ we have

$$
\log(1 - \hat{C}) = \frac{\sum_{i=1}^{s} z_i(F_i - \bar{F})}{\sum_{i=1}^{s} (F_i - \bar{F})^2}
$$

and

$$
\log \hat{N} = \bar{F}\log(1 - \hat{C}) - \log \hat{C}
$$

Parameter estimates of catchability ($\hat{C}$) and population size ($\hat{N}$) are obtained by taking antilogs. Seber (1982, 302) and Ricker (1975) show how confidence intervals may be calculated for these semilogarithmic models.

Since the Leslie model (equation [3.10]) and the Ricker model (equation [3.13]) are based on somewhat alternative approaches, it is desirable to plot both the Leslie regression (e.g., Figure 3.3) and the Ricker semilog regression (Figure 3.4) as checks on whether the underlying assumptions may be violated.
The program-group MARK-RECAPTURE (Appendix 2) can do these calculations for the catch-effort models of Leslie and Ricker described in this section; it calculates confidence intervals for population size for both estimators.

Population estimation by the removal method is subject to many pitfalls. Braaten (1969) showed by computer simulation that the DeLury (1947) semilogarithmic model produces population estimates that are biased by being too low on average. This bias can be eliminated by regressing the log of the catch-per-unit-effort against the accumulated fishing effort \( F_i \) plus half the effort expended in the \( i \)-interval \( (1/2 \ f_i) \) (Braaten 1969). The more serious problem of variable catchability has been discussed by Schnute (1983), who proposes a new method of population estimation for the removal method based on maximum-likelihood models. In particular, Schnute (1983) provides a method of testing for constant catchability and for fitting an alternate model in which catchability is higher in the first sample, and lower in all subsequent samplings. Otis et al. (1978) also discuss in detail the problem of removal estimation, in which the probability of capture varies with time. The critical assumption of constant catchability should always be examined when you use catch-effort methods to estimate population size.

3.2 RESIGHT METHODS

In recent work on vertebrate population, individuals are often marked with radio transmitters, and for such studies a range of new population estimators are available (Arnason et al. 1991; Neal et al. 1993; White 1996). Radio-tagged individuals are often expensive to capture and tag, but after they are released, they can be easily resighted using radio-telemetry equipment (Kennard 1987; White and Garrott 1990). The methods that have developed are an important extension of Petersen-type population estimators for closed populations. Resight methods do not require radio-telemetry, of course, and any marking method that allows one to identify an individual at a distance could be used with this approach.

Four estimators of population size are available for mark-resight data, and White (1996) has implemented these in Program NOREMARK. I discuss here only two of these four estimators, the joint hypergeometric maximum-likelihood estimator (JHE) and Bowden's estimator. The statistical theory behind the JHE estimator is beyond the scope of this book, but I provide a general understanding of how maximum-likelihood estimators are derived, since they form the core of much of modern estimation theory.

Maximum likelihood is a method of statistical inference in which a particular model is evaluated with reference to a set of data. In this case we have a set of observations based on the sighting frequencies of marked and unmarked animals. If we assume that resightings occur at random, we can connect through probability theory the observed data and the likely value of population size \( N \). For simple situations, such as the Petersen method, in which only two sampling times are involved, the resulting estimator for \( N \) will be a simple equation like equation (2.2). For more complex situations involving several sampling times, the resulting estimator cannot be written as a simple equation with a solution, and we must search to find the best value of \( N \) by trial and error. In mathematical jargon, we search for the maximum value of a function called the likelihood function (Edwards 1972). Figure 3.5 illustrates the maximum-likelihood approach for equation (3.14) and the data used in Box 3.2.
Figure 3.5 Likelihood ratio for the mountain sheep example given in Box 3.2. Given the observed data, estimated population sizes are substituted in equation (3.14) and the likelihood calculated. The most probable value of $N$ is that which gives the highest likelihood (arrow), in this case $N = 127$, at which point the log-likelihood is $-13.6746$ (likelihood $= 1.1513 \times 10^{-6}$). Because likelihoods cover a broad numerical range, it is easier to graph them as log-likelihoods ($\log(e)$ or $\ln$) as we have done here.

For the JHE estimator used by White (1996), we search for the value of $N$ that maximizes the following function:

$$L(N|M, n_i, m_i) = \prod_{i=1}^{k} \binom{M}{m_i} \binom{N-M}{n_i-m_i}$$

(3.14)

where $L(N|M, n_i, m_i) = \text{Likelihood of } N \text{ conditional on the observed values of } M, n_i \text{ and } m_i,$ and

- $N = \text{Population size}$
- $M = \text{Number of radio-marked animals in the study zone}$
- $n_i = \text{Total number of animals seen in the } i\text{-th sample survey } (i = 1, 2, 3 \ldots k)$
- $m_i = \text{Number of marked animals sighted in the } i\text{-th survey}$

and the operator $\binom{M}{m_i}$ indicates the number of possible combinations of $M$ items taken $m_i$ at a time $= M!/[m_i!(M - m_i)!].$
Box 3.2 Resight Method of Population Estimation

Neal et al. (1993) report the following data from radio-collared bighorn sheep (*Ovis canadensis*) from Trickle Mountain, Colorado, from 14 January to 1 February 1989:

<table>
<thead>
<tr>
<th>Date</th>
<th>Number of marked sheep, ( M_i )</th>
<th>Number of animals seen during survey, ( n_i )</th>
<th>Marked animals seen, ( m_i )</th>
</tr>
</thead>
<tbody>
<tr>
<td>January 14</td>
<td>25</td>
<td>40</td>
<td>9</td>
</tr>
<tr>
<td>January 17</td>
<td>25</td>
<td>63</td>
<td>11</td>
</tr>
<tr>
<td>January 18</td>
<td>25</td>
<td>66</td>
<td>14</td>
</tr>
<tr>
<td>January 19</td>
<td>25</td>
<td>57</td>
<td>11</td>
</tr>
<tr>
<td>January 27</td>
<td>25</td>
<td>52</td>
<td>10</td>
</tr>
<tr>
<td>January 28</td>
<td>25</td>
<td>61</td>
<td>9</td>
</tr>
<tr>
<td>February 1</td>
<td>25</td>
<td>87</td>
<td>19</td>
</tr>
</tbody>
</table>

There were a total of 426 recaptures in the sampling period, of which 83 sheep had radio-collars and 343 sheep were not marked. We can use each of these daily samples as Petersen estimates and obtain a series of Petersen estimates from equation (2.3). For example, from January 19 with \( M = 25 \), \( C = 57 \), and \( R = 11 \), using equation (2.3) for sampling with replacement, we obtain a Petersen estimate as follows:

\[
\hat{N} = \frac{M(C + 1)}{(R + 1)} = \frac{25(57 + 1)}{(11 + 1)} = 120.8 \text{ sheep}
\]

To use the radio method, we compute the likelihood of a range of possible values of \( N \) and find the one that has the maximum likelihood. This is tedious, and I illustrate only one calculation. Use as a preliminary estimate \( \hat{N} = 95 \). From equation (3.14),

\[
L(N | M, n_i, m_i) = \prod_{i=1}^{k} \left( \frac{M}{m_i} \right) \left( \frac{N - M}{n_i - m_i} \right)
\]

Since \( M = 25 \), we have seven terms to evaluate, as follows:

\[
L(95 | 25, n_i, m_i) = \frac{25}{9} \cdot \frac{95 - 25}{40 - 9} \cdot \frac{25}{11} \cdot \frac{95 - 25}{63 - 11} \cdot \frac{25}{14} \cdot \frac{95 - 25}{66 - 14} \cdots
\]

\[
= (0.14632) (0.00522) (0.04817) \cdots = 1.2318 \times 10^{-13}
\]
To avoid these very small numbers, we can express these likelihoods as log-likelihoods:

\[ \log_e (1.2318 \times 10^{-13}) = -29.7251 \]

Repeating these calculations for a range of values of \( N \) from 96 to 200 gives us the data plotted in Figure 3.5. The maximum likelihood occurs at \( \hat{N} = 127 \), which is the best estimate of population size given these resighting data. The 95\% confidence interval for this estimate from Program NOREMARK is 112 to 146.

For the Bowden estimator, we require the sighting frequencies of each of the 25 mountain sheep that had radio-transmitters. For these 25 animals, these values \( (f_i) \) were: 6, 4, 3, 6, 5, 3, 0, 5, 4, 6, 1, 0, 0, 5, 6, 0, 6, 1, 5, 5, 2, 2, 0, 4, and 4. From the usual statistical calculations and the variance equation above,

\[ \bar{f} = 3.320 \text{ resightings per animal} \]

\[ \text{VAR} (f_i) = 4.8576 \]

From equation (3.15) we obtain for these data

\[ \hat{N} = \frac{\left( \frac{u_T + m_T}{\bar{f}} \right) + \left( \frac{s^2}{\bar{f}^2} \right)}{1 + \left( \frac{s^2}{T \bar{f}^2} \right)} = \frac{\left( 343 + 83 \right) \div 3.320 + \left( \frac{4.8576}{(3.320)^2} \right)}{1 + \left( \frac{4.8576}{25(3.320)^2} \right)} = 126.52 \]

with the following variance from equation (3.16):

\[ \text{VAR} (\hat{N}) = \frac{N^2 \left( 1 - \frac{1}{N} \right) \left( \frac{s^2}{\bar{f}^2} \right)}{\left( 1 + \frac{s^2}{T \bar{f}^2} \right)^2} = \frac{126.52^2 \left( \frac{1}{25} - \frac{1}{126.52} \right) \left( \frac{4.8576}{3.320^2} \right)}{1 + \left( \frac{4.8576}{25(3.320)^2} \right)^2} = 218.658 \]

The 95\% confidence limits from equations (3.17) and (3.18) are, with \( t_\alpha = 2.064 \) for 24 degrees of freedom,

Lower confidence limit \( = \frac{\hat{N}}{\exp[t_\alpha CV(\hat{N})]} = \frac{126.52}{e^{(2.064(\sqrt{218.658/126.52})}}} = 99 \)

Upper confidence limit of \( \hat{N} = (\hat{N}) \{ \exp[t_\alpha CV(\hat{N})] \} = (126.52)e^{(2.064(\sqrt{218.658/126.52})}) \]

\[ = 161 \]

Note that these confidence limits are slightly wider than those given for the JHE estimator above. This is the price we pay for the less restrictive assumption that individual sheep may have different probabilities of being sighted on the study area.

These calculations are done by program-group MARK-RECAPTURE (Appendix 2) and by Program NOREMARK from White (1994).
Equations of this type for many maximum-likelihood estimators can be solved only by trial and error, by substituting values of \( N \) into the equation and finding the value that maximizes the likelihood. For this reason all these methods are computer-intensive and were not feasible before the advent of modern computers.

Radio estimators can be viewed as a weighted overall average of a series of Petersen estimates for each sampling period. Box 3.2 illustrates the application of the radio method to sample data on radio-collared mountain sheep.

Confidence intervals for the JHE estimator can be determined by the profile-likelihood method described by Venzon and Moolgavkar (1988). These methods are computer-intensive and will not be described here.

The radio method assumes that all the marked animals remain on the study area during the surveys. Thus the number of marked animals is constant, although the probability of resighting need not be constant from sample to sample. Day-to-day variation in sightability can thus be accommodated in this model.

Bowden and Kufeld (1995) developed an estimate for population size with radio data that allows us to relax the assumption that all individuals in the population have the same probability of resighting. To compute this estimator, we need to have the resighting frequency for each radio-tagged individual in the population. Some animals may not be seen at all, and some may be seen at every one of the sampling times. The Bowden estimator of population size is given by

\[
\hat{N} = \frac{\left( \frac{u_T + m_T}{f} \right) + \left( \frac{s_f^2}{f^2} \right)}{\left[ 1 + \left( \frac{s_f^2}{Tf^2} \right) \right]} \tag{3.15}
\]

where

- \( u_T = \) Total number of sightings of unmarked animals over all time periods
- \( m_T = \) Total number of sightings of marked animals over all time periods
- \( \bar{f} = \) Mean resighting frequency of marked animals = \( m_T / T \)
- \( T = M = \) Number of marked animals in the population at the time of the surveys
- \( s_f^2 = \) Variance of sighting frequencies of marked animals = \( \sum_{i=1}^{T} (f_i - \bar{f})^2 / T \)

Note that the variance estimate for sighting frequencies has \( T \) in the denominator (and not \( T - 1 \)) because it is a complete sample of all the population of radio-tagged animals.

This estimate (3.15) has the following variance:

\[
\text{Var}(\hat{N}) = \frac{\hat{N}^2 \left( \frac{1}{T} - \frac{1}{N} \right) \left( \frac{s_f^2}{f^2} \right)}{\left( 1 + \frac{s_f^2}{Tf^2} \right)^2} \tag{3.16}
\]
Confidence intervals for the Bowden estimator are obtained from a log-transformation as

\[
\text{Lower confidence limit} = \frac{\hat{N}}{\exp[t_\alpha \text{CV}(\hat{N})]} \tag{3.17}
\]

\[
\text{Upper confidence limit of } \hat{N} = (\hat{N})\{\exp[t_\alpha \text{CV}(\hat{N})]\} \tag{3.18}
\]

where \( t_\alpha \) = \( t \)-value with \((T - 1)\) degrees of freedom for the specified confidence level, and

\[
\text{CV}(\hat{N}) = \text{coefficient of variation of } (\hat{N}) = \frac{\sqrt{\text{Var}(\hat{N})}}{\hat{N}} \tag{3.19}
\]

The Bowden estimator usually gives somewhat wider confidence limits for the population estimate because it does not make the restrictive assumption that all individuals have equal sightability. It can be computed with program-group MARK-RECAPTURE (Appendix 2) or in Program NOREMARK from White (1996).

3.3 COMPUTER PROGRAMS FOR POPULATION ESTIMATORS

Estimation methods for closed populations have been unified by the approaches outlined in the monograph by Otis et al. (1978). These methods complement the estimators discussed in Chapter 2 for closed populations, but they are more restrictive because they assume that every marked animal can be individually recognized and that at least three sampling periods were used. These methods are all computer-intensive and have been codified in Program CAPTURE and Program MARK for the IBM PC.* I will discuss here only the basic outline of these methods and indicate the data needed for these calculations.

The simplest form of data input is in the form of an X matrix. The rows of this matrix represent the individual animals that were captured in the study, and the columns of the matrix represent the time periods of capture. In each column a 0 (zero) indicates that the individual in question was not caught during this sampling time, and a 1 (one) indicates that the individual was captured. A sample X matrix is as follows:

<table>
<thead>
<tr>
<th>Tag number</th>
<th>Time 1</th>
<th>Time 2</th>
<th>Time 3</th>
<th>Time 4</th>
<th>Time 5</th>
<th>Time 6</th>
<th>Time 7</th>
</tr>
</thead>
<tbody>
<tr>
<td>3455</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>3456</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>3458</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>3462</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>3463</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>3476</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>3488</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
</tbody>
</table>

This indicates that animal tag number 3455 was caught in the first trapping session but not caught in the second or third session, caught in the fourth, fifth, and sixth sessions but not

*These programs are currently available from Colorado State University at www.cnr.colostate.edu/~gwhite/software.html.
in the seventh. In a normal study these catching sessions might represent one day but they
could be one hour or one week or whatever sampling time unit is appropriate to your
animals.

Given the matrix of 0's and 1's, it is possible to use probability theory to ask how
these should be arranged under several different models of capture behavior. The simplest
model is the null model, in which the captures occur completely at random with respect to
all individuals and all individuals have equal chances of being caught at any time. The null
model in Program CAPTURE is essentially the equivalent of the Petersen and Schnabel
models discussed in Chapter 2. If the null model does not fit the observed data well, there
are three primary sources of variation that can cause changes in capture probabilities:

1. **Time**: The probability of capture varies with the time of capture. If it rains one
day, the capture rate may be lower than usual (or higher depending on the species).
2. **Heterogeneity**: Individual animals may differ in the propensity to be caught,
so that some individuals are trap-happy and some are trap-shy. Alternatively,
some animals move around more and are exposed to more traps. This individual
variation in chances of capture is called *heterogeneity*, and it is an important
source of violation of the equal catchability assumption that many mark-recapture
models make.
3. **Behavior**: Individual animals may change their behavior after they are caught
once, so that the chances of capture may be quite different for the first capture and
all subsequent captures. This source of variation is also common and is labeled
behavior because it arises in general as a behavioral response of animals to the
trapping devices.

These sources of variation can be combined to produce a model that includes both *time* and
*heterogeneity*, and the shorthand used by Otis et al. (1978) is to label this Model $M_{TH}$.
There are thus eight possible models that might be used in Program CAPTURE:

- $M_0$: the null model
- $M_T$: the time model (Darroch)
- $M_H$: the heterogeneity model (Jackknife)
- $M_B$: the behavior model (Zippin)
- $M_{TH}$: the time and heterogeneity model
- $M_{TB}$: the time and behavior model
- $M_{BH}$: the behavior and heterogeneity model (Generalized Removal)
- $M_{T淮}$: the full model with time, heterogeneity, and behavior varying

The more complicated models, as you might guess, are harder to fit to observed data, and
at present no one has solved the full model $M_{T淮}$; therefore, it cannot be utilized.

The key problem remaining is which of these models to use on your particular data.
Otis et al. (1978) have devised a series of chi-squared tests to assist in this choice, but these
do not give a unique answer with most data sets. Work is continuing in this area to develop
better methods of model selection.

The details of the models and the calculations are presented in Otis et al. (1978). For
ecologists, a general description of the procedures used and some sample data runs are
given in White et al. (1982). Maximum-likelihood methods are used in all the estimation
procedures in CAPTURE, similar to those described above for the RESIGHT method, and
I will illustrate only one method here, the null model $M_0$. The best estimate of $\hat{N}$ for model
$m_0$ is obtained from the following maximum-likelihood equation:

$$L(\hat{N}_0, p | X) = \ln \left( \frac{N!}{(N - M)!} \right) + (n) \ln(n) + (tN - n) \ln(tN - n) - (tN) \ln(tN)$$

(3.20)

where $\hat{N}_0 = $ Estimated population size from the null model of CAPTURE
$N = $ Provisional estimate of population size
$p = $ Probability of capture
$M = $ Total number of different individuals captured in the
entire sampling period
$n = $ Total number of captures during the entire sampling period
$t = $ Number of samples (e.g., days)
$\ln = $ Natural log ($\log_e$)
$L = $ Log-likelihood of the estimated value $\hat{N}_0$ and $p$, given the
observed $X$ matrix of captures

This equation is solved by trial and error to determine the value of $N$ that maximizes the
log-likelihood (as in Figure 3.5), and this value of $N$ is the best estimate of population size.

Once the value of $\hat{N}_0$ has been determined, the probability of capture can be ob-
tained from

$$\hat{p} = \frac{n}{t\hat{N}_0}.$$  \hspace{1cm} (3.21)

and the variance of the estimated population size is obtained from

$$\text{Var}(\hat{N}_0) = \frac{\hat{N}_0}{(1 - \hat{p})^{-1} - (t/1 - \hat{p}) + t - 1}.$$  \hspace{1cm} (3.22)

The standard error of this population estimate is the square root of this variance, and hence
the confidence limits for the estimated population size are given by the usual formula:

$$\hat{N}_0 \pm z_\alpha \sqrt{\text{Var}(\hat{N}_0)}$$

(3.23)

where $z_\alpha = $ Standard normal deviate (i.e., 1.960 for 95% confidence limits,
2.576 for 99% limits, or 1.645 for 90% limits)

Because these confidence limits are based on the normal distribution, there is a tен
dency for confidence intervals of population estimates to be more narrow than they ought
to be (Otis et al. 1978, 105).

The null model $M_0$ has a simple form when there are only two sampling periods (as
in a Petersen sample). For this situation, equation (3.20) simplifies to

$$\hat{N}_0 = \frac{(n_1 + n_2)^2}{4m}$$

(3.24)

where $n_1 = $ Number of individuals captured in the first sample and marked
$n_2 = $ Number of individuals captured in the second sample
$m = $ Number of recaptured individuals in the second sample
Box 3.3 Null Model of Program Capture to Estimate Population Size for Humpback Whales

Palsbøll et al. (1997) reported on mark-recapture studies of humpback whales (*Megaptera novaeangliae*) in the North Atlantic Ocean. For the Gulf of St. Lawrence subpopulation, they captured 65 genetically distinct individuals, and over 5 sampling periods they tallied 86 sightings (sampling with replacement).

To illustrate how Program CAPTURE calculates a population estimate, we use these data with the null model, which assumes no heterogeneity in capture probabilities, no time variation in catchability, and no behavioral changes as a result of the original capture of a genetic sample for identification.

Given a provisional range of estimates of population size, the method of maximum likelihood is used to find the most likely estimate of \( N \). From equation (3.20),

\[
L(\hat{N}_0, \hat{p} | X) = \ln \left( \frac{N!}{(N-M)!} \right) + (n)\ln(n) + (tN - n)\ln(tN - n) - (tN)\ln(tN)
\]

where
- \( \hat{N}_0 \) = Estimated population size from the null model of CAPTURE
- \( N \) = Provisional estimate of population size
- \( \hat{p} \) = Probability of capture
- \( M \) = Total number of different individuals captured in the entire sampling period
- \( n \) = Total number of captures during the entire sampling period
- \( t \) = Number of samples (e.g., days)
- \( \ln \) = Natural log (\( \log_e \))
- \( L \) = Log-likelihood of the estimated value \( \hat{N}_0 \) and \( p \), given the observed data

A great deal of computation goes into finding the maximum of this function, and I illustrate here only one set of calculations to show in principle how the method works.

Use 112 for a provisional estimate of population size (\( N \)). Calculate the log-likelihood as

\[
L(\hat{N}_0, \hat{p} | X) = \ln \left( \frac{112!}{(112-65)!} \right) + (86)\ln(86) + (5[112] - 86)\ln(5[112] - 86)
\]

\[
- (5[112])\ln(5[112])
\]

\[
= 42.789
\]

By repeating this calculation for other provisional estimates of \( N \), you can determine

for \( N = 117 \), \( L(\hat{N}_0, \hat{p} | X) = 42.885 \)

for \( N = 121 \), \( L(\hat{N}_0, \hat{p} | X) = 42.904 \)

for \( N = 126 \), \( L(\hat{N}_0, \hat{p} | X) = 42.868 \)

and the maximum likelihood occurs at \( \hat{N} \) of 121 whales.
Note that in practice you would use Program CAPTURE to do these calculations and also to test whether more complex models involving variation in probability of capture due to time or behavior might be present in these data.

The probability of an individual whale being sighted and sampled for DNA at any given sample period can be determined from equation (3.21):

\[
\hat{p} = \frac{n}{t\hat{N}_0} = \frac{86}{5(121)} = 0.142
\]

Given this probability, we can now estimate the variance of population size from equation (3.22)

\[
\text{Var}(\hat{N}_0) = \frac{\hat{N}_0}{(1 - \hat{p})^{t} - (t/1 - \hat{p}) + t - 1}
\]

\[
= \frac{121}{(1 - 0.142)^{-5} - [5/(1 - 0.142)] + 5 - 1} = 373.5
\]

and the resulting 90% confidence interval from equation (3.23) is

\[
\hat{N}_0 \pm z_a \sqrt{\text{Var}(\hat{N}_0)}
\]

\[
121 \pm 1.645 \sqrt{373.5 \text{ or } 121 \pm 32}
\]

These calculations, including confidence limits, can be done by Program CAPTURE, and this method is discussed in detail by Otis et al. (1978).

For example, from the data in Box 2.1, the null model estimate of population size is

\[
\hat{N}_0 = \frac{(n_1 + n_2)^2}{4m} = \frac{(948 + 421)^2}{4(167)} = 2806 \text{ hares}
\]

This estimate is 18% higher than the Petersen estimate calculated in Box 2.1. The null model tends to be biased towards overestimation when the number of sampling times \(t\) is less than 5, unless the proportion of marked animals is relatively high. For this reason the Petersen method is recommended for data gathered over two sampling periods, as in this example. Program CAPTURE and Program MARK become most useful when there are at least 4–5 sampling times in the mark-recapture data, and like all mark-recapture estimators, they provide better estimates when a high fraction of the population is marked.

Box 3.3 gives a sample set of calculations for the null model from Program CAPTURE.

### 3.4 ENUMERATION METHODS

Why estimate when you can count the entire population? This is one possible response to the problems of estimating density by mark-recapture, removal, or resight methods. All of these methods have their assumptions, and you could avoid all this statistical hassle by counting all the organisms in the population. In most cases this simple solution is not...
possible either physically or financially, and you must rely on a sampling method of some type, but in a few situations, enumeration is a possible strategy.

Enumeration methods have been used widely in small mammal studies (Krebs 1966) where they have been called the minimum-number-alive method (MNA). The principle of this method is simple. Consider a small example from a mark-recapture study (0 = not caught, 1 = caught):

<table>
<thead>
<tr>
<th>Tag number</th>
<th>Time 1</th>
<th>Time 2</th>
<th>Time 3</th>
<th>Time 4</th>
<th>Time 5</th>
</tr>
</thead>
<tbody>
<tr>
<td>A34</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>A38</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>A47</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>A78</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>A79</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>A83</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>No. caught</th>
<th>Minimum number alive</th>
</tr>
</thead>
<tbody>
<tr>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>3</td>
<td>5</td>
</tr>
<tr>
<td>4</td>
<td>6</td>
</tr>
<tr>
<td>3</td>
<td>6</td>
</tr>
<tr>
<td>5</td>
<td>5</td>
</tr>
</tbody>
</table>

Individuals miss being caught at one or more sample periods, but if they are known to be present before and after the time of sampling, we assume they were present but not caught during the intervening sample times. These individuals are added to the number actually caught to give the minimum number alive—simple arithmetic, no complicated equations, and apparently an ecologist’s dream!

Enumeration methods have been used for birds, small mammals, reptiles, and amphibians (Pollock et al. 1990), and their simplicity makes them popular. But there is one overwhelming complaint about enumeration methods—they all suffer from a negative bias. Numbers enumerated are always less than or equal to the true population size (Jolly and Dickson 1983). If catchability is high, so that most individuals are caught in most of the sampling periods, this negative bias is small. But if catchability is low, the negative bias is very large.

The net result is that enumeration methods should not be used when it is practical to use one of the unbiased mark-recapture methods. At the very least we should compute both, for example, the Jolly-Seber population estimates and the MNA estimates, and show that these are nearly the same. Jolly-Seber estimates can never be below MNA estimates, and these two will converge only when all animals are caught each sampling time.

In a few cases enumeration methods are needed and can be justified on the principle that a negatively biased estimate of population size is better than no estimate. In some cases the numbers of animals in the population are so low that recaptures are rare. In cases with endangered species, it may not be possible to mark and recapture animals continuously without possible damage, so sample sizes may be less than the 5–10 individuals needed for most estimators to be unbiased. In these cases it is necessary to ask whether a population estimate is needed, or whether an index of abundance is sufficient for management purposes. It may also be possible to use the methods presented in the next two chapters for rare and endangered species. The important point is to recognize that complete enumeration is rarely a satisfactory method for estimating population size.

The fact that most animals do not satisfy the randomness-of-capture assumption of mark-recapture models is often used to justify the use of enumeration as an alternative
estimation procedure. But Pollock et al. (1990) show that even with heterogeneity of capture, the Jolly-Seber model is less biased than MNA-based enumeration procedures. A closed population estimator or the Jolly-Seber model should be used in almost all cases instead of enumeration.

3.5 ESTIMATING DENSITY

We have been discussing methods of estimating abundance, and yet most ecologists want to know the density of the population, the number of individuals per unit area or unit volume. If you know the size of the study area, it is easy to determine the density once you know the abundance of a species. But in many cases the transition from abundance to density is far from simple. Consider, for example, a grouse population in an extensive area of forest or moorland. Individuals captured and marked on the study area will move on and off the area, and the home ranges of vertebrates may be only partly on the study area. In practice this means that the size of the study area is larger than the physical area trapped, and the true population density is less than the biased density estimate obtained by dividing the population estimate by the physical area of study. Figure 3.6 illustrates the problem.

Figure 3.6 The trapping grid (square) includes all, part, or none of the home ranges of the animals in the study zone. Some of the animals whose home ranges overlap the trapping grid will be captured, marked, and released. The effective size of the trapping grid is thus larger than its physical area. If home ranges are very small, the effective grid area is only slightly larger than its physical area. (Modified from White et al. 1983.)
schematically. How can we determine how large an effective area we are studying so that we can obtain estimates of true density? Several methods have been employed to estimate the effective size of a trapping area.

### 3.5.1 Boundary Strip Methods

The simplest methods add a boundary strip around the trapping area to estimate the effective size of area trapped. Figure 3.7 illustrates the principle of a boundary strip. The width of the boundary strip can be estimated in several ways (Stenseth and Hansson 1979). The simplest procedure is to add a strip one-half the movement radius of the animals under study. For example, for mammals, we can determine the average distance moved between trap captures and use this as a likely estimate of movement radius. The problem with this approach is that it is highly dependent on the spacing between the capture points and the number of recaptures. While this approach is better than ignoring the problem of a boundary strip, it is not completely satisfactory (Otis et al. 1978).

A more sophisticated boundary strip method was devised by Bondrup-Nielsen (1983), who used home range size to estimate effective size of a sampling area. The general principle is to try to minimize the boundary strip effect by defining the required size of the sampling area. This method proceeds in three steps:

1. Calculate the average home range size for the animal under study. Methods for doing this are presented in Kenward (1987) and in White and Garrott (1990).

![Image](image_url)  
**Figure 3.7** Illustration of a study grid of $10 \times 10$ checkerboard shape with a boundary strip added to delineate the effective study area. Population size would be estimated for the checkerboard, and the total area, including the boundary strip, would be used to estimate population density.
2. Compute the ratio of grid size to area of the average home range. In a hypothetical world with square home ranges that do not overlap, the overestimation of density is shown by Bondrup-Nielsen (1983) to be

\[
\frac{\text{Estimated density}}{\text{True density}} = \frac{(\sqrt{A} + 1)^2}{A} \tag{3.25}
\]

where \[ A = \frac{\text{Area of study grid}}{\text{Average home range size}} \tag{3.26} \]

3. Assume that the home range is elliptical, and use a computer to “throw” home ranges at random on a map that delineates the study zone as part of a large area of habitat.

Figure 3.8 shows the results of this simulation. On the basis of this graph, Bondrup-Nielsen (1983) suggested that the trapping grid size should be at least 16 times the size of the average home range of the species under study to minimize the edge effect.

Given that we have data on study area size and average home range size, we can use Figure 3.8 as a guide to estimating true density of a population. For example, in a study of house mouse populations in wheat fields, live traps were set out on a 0.8 ha grid, and the Petersen population estimate was 127 mice. The average home range size of these house
mice was 0.34 ha. We can calculate as follows from equation (3.26):

\[ A = \frac{\text{Grid size}}{\text{Home range size}} = \frac{0.8}{0.34} = 2.35 \]

From Figure 3.8 or equation (3.25) the expected overestimate is

\[ \frac{\text{Estimated density}}{\text{True density}} = \frac{(\sqrt{A} + 1)^2}{A} = \frac{(\sqrt{2.35} + 1)^2}{2.35} = 2.73 \]

Thus the biased density estimated from the area of the grid is

\[ \text{Biased density estimate} = \frac{\text{Population estimate}}{\text{Size of study area}} = \frac{127 \text{ mice}}{0.8 \text{ ha}} = 159 \text{ mice per ha} \]

\[ \text{Corrected density estimate} = \frac{159}{2.73} = 58 \text{ mice per ha} \]

This correction factor is only approximate because home ranges are not exactly elliptical, and there is some overlap among individuals, but the adjusted density estimate is closer to the true value than is the biased estimate that does not take into account the effective grid size.

### 3.5.2 Nested Grids Method

A more rigorous method for estimating density was developed by Otis et al. (1978). If a large area is sampled, it may be possible to break the data up into a series of nested grids (Figure 3.9). At least 4 nested grids are needed to get good estimates, and this will mean a 15 × 15 checkerboard of sample traps or capture points. The principle of the method is simple: The biased density estimate (population estimate/size of sampling area) will decline as the sampling area increases in size. Each nested grid will have a larger and larger area of boundary strip as grid size increases (Figure 3.9), and we can use the change in observed density to estimate the width of the boundary strip for the population being studied.

The estimation problem is difficult, and the details are not given here (see Otis et al. 1978). Given the area and the population estimate for each subgrid, the problem is to estimate two parameters: boundary strip width and population density. If the boundary strip is very wide, the biased density estimates will change very slowly with grid size. Figure 3.10 illustrates an example from Richardson's ground squirrels in which biased density falls rapidly with grid size. The estimation procedures are available in Program CAPTURE (described above).

There is some controversy about the utility of the nested grids approach to estimating population density. Few trials have been done on field populations, and some of these have provided accurate density estimates (Wilson and Anderson 1985a). Computer-simulated populations however typically show a large positive bias in the density estimate because the strip width is underestimated (Wilson and Anderson 1985b).

The nested grids approach to density estimation is very data-intensive, and it works best when a high fraction of the population can be marked and recaptured and when density
Figure 3.9  An example of a set of nested grids for population density estimation. The entire study area is a $17 \times 17$ checkerboard, and 4 nested subgrids are shown by the lines. The nested grids are $5 \times 5$, $9 \times 9$, $13 \times 13$, and $17 \times 17$, and if the sample points are 10 m apart (for example), the areas of these four subgrids would be 0.16 ha, 0.64 ha, 1.44 ha, and 2.56 ha.

Figure 3.10  Illustration of the approach to density estimation from nested grids. Data on Richardson’s ground squirrels live-trapped on a $10 \times 10$ checkerboard grid with 10 m spacing. Four nested subgrids of $4 \times 4$, $6 \times 6$, $8 \times 8$ and $10 \times 10$ were used to generate four separate estimates of population size. The biased density estimate (population estimate/area trapped) declines with grid size. The best estimate of true density for these data was 45 squirrels per hectare, with a boundary strip width of 12.4 m. These estimates were obtained using Program CAPTURE. (Data from White et al. 1983.)
is moderate to high. It assumes that the density of the population is uniform over all the area of the nested grids, and that the population is closed during the time of sampling. If the traps used are attractive to animals, so that individuals are attracted into the study area, the assumption that the population is closed will be violated, and this method should not be used. If a removal study is being conducted, and the removal extends over a long period so that immigrants enter the population, again the assumption of a closed population is violated, and this method is not useful.

### 3.5.3 Trapping Web Method

A third approach to density estimation was suggested by Anderson et al. (1983) and has been called the trapping web design. This method is described only briefly here, since it depends on distance methods that are discussed in Chapter 5. It was designed primarily for small mammals that are sampled by live-trapping, but it could be adapted to any species of limited mobility. The layout of the trapping web is shown in Figure 3.11. This method assumes that all individuals at the center of the web are captured. Radial lines of 15–20 traps are laid out as spokes on a wheel, and trap density is adjusted so that there are at least 8–12 traps in every home range at the center of the web. The critical assumption is that every individual in the center of the web is captured.

The data obtained from this design are the numbers of individuals captured in each of the trapping rings. As you move away from the center of the web, the area of each successive ring is larger, and consequently the trap density is lower. The expectation is that the number of individuals caught will increase in the outer rings of the web. This method is a type of removal method, because each individual is counted only the first time it is caught and marked, and all recaptures are ignored.

The details of the calculations for the density estimate are given in Chapter 5 and are covered in Anderson et al. (1983). In addition to the assumption that all individuals in the center of the web are caught, this method assumes that the distances from the center of the web to each trap are measured accurately, and that animals are not attracted to the traps from outside the web. If there is some attraction to the traps, it is possible to throw away the data from the outer 2 or 3 rings. The suggested configuration of the trapping web is to have 16 lines with at least 16 traps in each line of the web. Approximately 60 individuals or more are needed to obtain a reasonably precise estimate of density (Anderson et al. 1983).

### 3.6 SUMMARY

Three special techniques are presented in this chapter that may be useful for population estimation with exploited populations. If there are two types of organisms in a population, like males and females, and hunting removes more of one type than the other, the resulting change-in-ratio may be used to estimate population size. Large samples are usually required for change-in-ratio estimators, and you need to plan your sampling program thoroughly. Alternatively, if removals are not sex- or age-specific, you can use Eberhardt’s index-removal method to estimate population size. This method depends on index counts that must enumerate about 20% or more of the total population to achieve precise estimates of population size.
implemented in two programs for personal computers. They are restrictive in assuming closed populations and at least 3 (and typically 5) capture periods, and they require individual capture histories to be recorded for all animals.

Enumeration methods have a long history in population ecology, and their simplicity makes them attractive. But all methods of enumeration suffer from a negative bias—population estimates are always less than or equal to the true population—and they should be used only as a last resort. The critical assumption of enumeration methods is that you have captured or sighted all or nearly all of the animals in the population, so that the bias is minimal. Enumeration methods may be required for endangered species that cannot be captured without trauma.

All of the methods in this chapter and the previous chapter estimate population size, and to convert this to population density, you must know the area occupied by the population. This is simple for discrete populations on islands but difficult for species that are spread continuously across a landscape. Nested grids may be used to estimate density, or a boundary strip may be added to a sampling area to approximate the actual area sampled. For small mammals, a trapping web design may be used for density estimation. Density estimates are more reliable when the sampling area is large relative to the home range of the animal being studied and when a large fraction of the individuals can be captured.

SELECTED READING


QUESTIONS AND PROBLEMS

3.1. For the catch-effort regression estimation technique of Leslie, discuss the type of bias in estimated population size when there is

(a) Change in catchability during the experiment.

(b) Natural mortality during the experiment.
(c) Mortality caused by the marking procedure or the tag itself.
(d) Emigration of animals from the population.

3.2. Leslie and Davis (1939) set 210 rat traps (break-back type) in 70 houses in Freetown, Sierra Leone, in 1937. They caught, over 18 days,

<table>
<thead>
<tr>
<th>Day</th>
<th>No. of <em>Rattus rattus</em> caught</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>49</td>
</tr>
<tr>
<td>2</td>
<td>32</td>
</tr>
<tr>
<td>3</td>
<td>31</td>
</tr>
<tr>
<td>4</td>
<td>34</td>
</tr>
<tr>
<td>5</td>
<td>16</td>
</tr>
<tr>
<td>6</td>
<td>33</td>
</tr>
<tr>
<td>7</td>
<td>22</td>
</tr>
<tr>
<td>8</td>
<td>27</td>
</tr>
<tr>
<td>9</td>
<td>17</td>
</tr>
<tr>
<td>10</td>
<td>19</td>
</tr>
<tr>
<td>11</td>
<td>18</td>
</tr>
<tr>
<td>12</td>
<td>16</td>
</tr>
<tr>
<td>13</td>
<td>18</td>
</tr>
<tr>
<td>14</td>
<td>12</td>
</tr>
<tr>
<td>15</td>
<td>14</td>
</tr>
<tr>
<td>16</td>
<td>12</td>
</tr>
<tr>
<td>17</td>
<td>17</td>
</tr>
<tr>
<td>18</td>
<td>7</td>
</tr>
</tbody>
</table>

They set 210 traps each day. Estimate the total population size of *Rattus rattus* at the start of the study. What sources of error might affect this particular estimate?

3.3. During a severe winter in 1938–39 in Utah, mule deer populations suffered heavy losses from starvation. The ratio of fawns to adults was 83 fawns to 100 adults before the severe weather (n=69 and 83 observed), and 53 fawns and 100 adults after the winter (n=38 and 72). Over the study area, 248 dead fawns and 60 dead adults were found, and these were believed to represent the whole of the losses (Rasmussen and Doman 1943). Estimate population size for this deer population at the start and end of this winter. Calculate 95% confidence intervals for your estimates.

3.4. Dunnet (1963) sampled quokkas (small marsupials) on Rottnest Island off Western Australia over three sampling periods with these results for 1957:

<table>
<thead>
<tr>
<th></th>
<th>Mature animals</th>
<th>Immature animals</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number marked at time 1</td>
<td>32</td>
<td>35</td>
</tr>
<tr>
<td>Number marked at time 1</td>
<td>22</td>
<td>20</td>
</tr>
<tr>
<td>and never seen again</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number marked caught</td>
<td>5</td>
<td>1</td>
</tr>
<tr>
<td>at times 1 and 2 only</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number marked caught</td>
<td>4</td>
<td>11</td>
</tr>
<tr>
<td>at times 1 and 3 only</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number marked caught</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>at times 1, 2, and 3</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Recast these data in the form of an X matrix, and use Program CAPTURE to estimate the size of the mature population and the immature population of this marsupial. What model is selected
by Program CAPTURE, and how different are the estimates from the different models available in this program? Does the test in Program CAPTURE suggest any evidence for unequal catchability in these data?

3.5. Plan a study that will use the change-in-ratio estimator of population size. You would like to get an estimate within ±10% of the true value at an α of 5%. You expect a change in the proportion of males in your population to be about 10–15%. Describe your proposed sampling program in detail. How is it affected by uncertainty about the initial sex ratio (which might be from 50% males to 70% males)? How is it affected by the rate of exploitation?

3.6. White-footed mice were live-trapped in northern Michigan by Blair (1942). He trapped a large area of 7.4 ha. The population estimate was 39 males and 31 females for this trapping area. Male white-footed mice have home ranges that average 0.93 ha, while females have smaller ranges (0.56 ha). What are the biased density estimates for the two sexes of mice for this particular area, and what are the best estimates of the true density for each sex? What size of live-trapping area would you recommend for this species?

3.7. An aerial index count of feral water buffalo in the Northern Territory of Australia was carried out before and after a culling program in 1984. In the first index count 2786 buffalo were counted, and in the second count 1368 were seen. The cull occurred over two months, and 12,890 buffalo were shot. Can you estimate population size for this population? What proportion of the population was culled? What assumptions must you make to use these estimates?

3.8. During 7 aerial flights to locate 19 radio-collared caribou in southern British Columbia over a 2-week period, a total of 144 caribou were seen, of which 54 had radio-collars and the remaining 90 were not marked. The frequency of resighting of the 19 collared caribou was as follows: 7, 5, 1, 2, 3, 0, 5, 3, 1, 3, 0, 2, 4, 6, 1, 5, 1, 3, and 2. Estimate the population size of this caribou herd and the 90% confidence limits for this estimate.

3.9. Discuss from a practical point of view the advantages and disadvantages of using a trapping web design versus a nested grid design to estimate population density for a small mammal. What information might be lost if you adopted one design over the other?