

PART ONE

ESTIMATING ABUNDANCE IN ANIMAL AND PLANT POPULATIONS

How many are there? This question is the central question of many ecological studies. If you wish to harvest a lake trout population, one helpful bit of information is the size of the population you wish to harvest. If you are trying to decide whether to spray a pesticide for aphids on a crop, you may wish to know how many aphids are living on your crop plants. If you wish to measure the impact of lion predation on a zebra population, you will need to know the size of both the lion and the zebra populations.

The cornerstone of many ecological studies is an estimate of the abundance of a particular population. This is true for both population ecology, in which interest centers on individual species, and community ecology, in which interest centers on groups of species and, thus, the estimation problem is more complex. Note that some ecological studies do not require an estimate of abundance, so before you begin with the labor of estimating the size of a population, you should have a clear idea why you need these data. Estimates of abundance themselves are not valuable, and a large book filled with estimates of the abundance of every species on earth as of January 1, 1997 would be a good conversation piece but not science.

Abundance can be measured in two ways. *Absolute density* is the number of organisms per unit area or volume. A red deer density of four deer per square kilometer is an absolute density. *Relative density* is the density of one population relative to that of another population. Blue grouse may be more common in a block of recently burned woodland than in a block of mature woodland. Relative density estimates are usually obtained with some biological index that is correlated with absolute density. Relative density may be adequate for many ecological problems, and should always be used when adequate because it is much easier and cheaper to determine than absolute density.

Absolute density must be obtained for any detailed population study in which one attempts to relate population density to reproductive rate, or any other vital statistic. The analysis of harvesting strategies may demand information on absolute numbers. All community studies which estimate energy flow or nutrient cycles require reliable estimates of absolute density.

The sequence of decisions by which one decides how to estimate absolute density is outlined in Figure A. Many factors - ecological, economic, and statistical - enter into a decision about how to proceed in estimating population size. Figure A thus gives relative guidance rather than absolute rules. Quadrat counts and spatial distribution methods are usually chosen in plant studies. Many vertebrate studies use mark-recapture techniques. Fish and wildlife populations that are exploited can be estimated by a special set of techniques applicable to harvested populations. There is a rapidly accumulating store of ecological wisdom for estimating populations of different animal and plant species, and if you are assigned to study elephant populations, you should begin by finding out how other elephant ecologists have estimated population size in this species. But do not stop there. Read the next five chapters and you may find the conventional wisdom needs updating. Fresh approaches and new improvements in population estimation occur often enough that ecologists cannot yet become complacent about knowing the best way to estimate population size in each species.

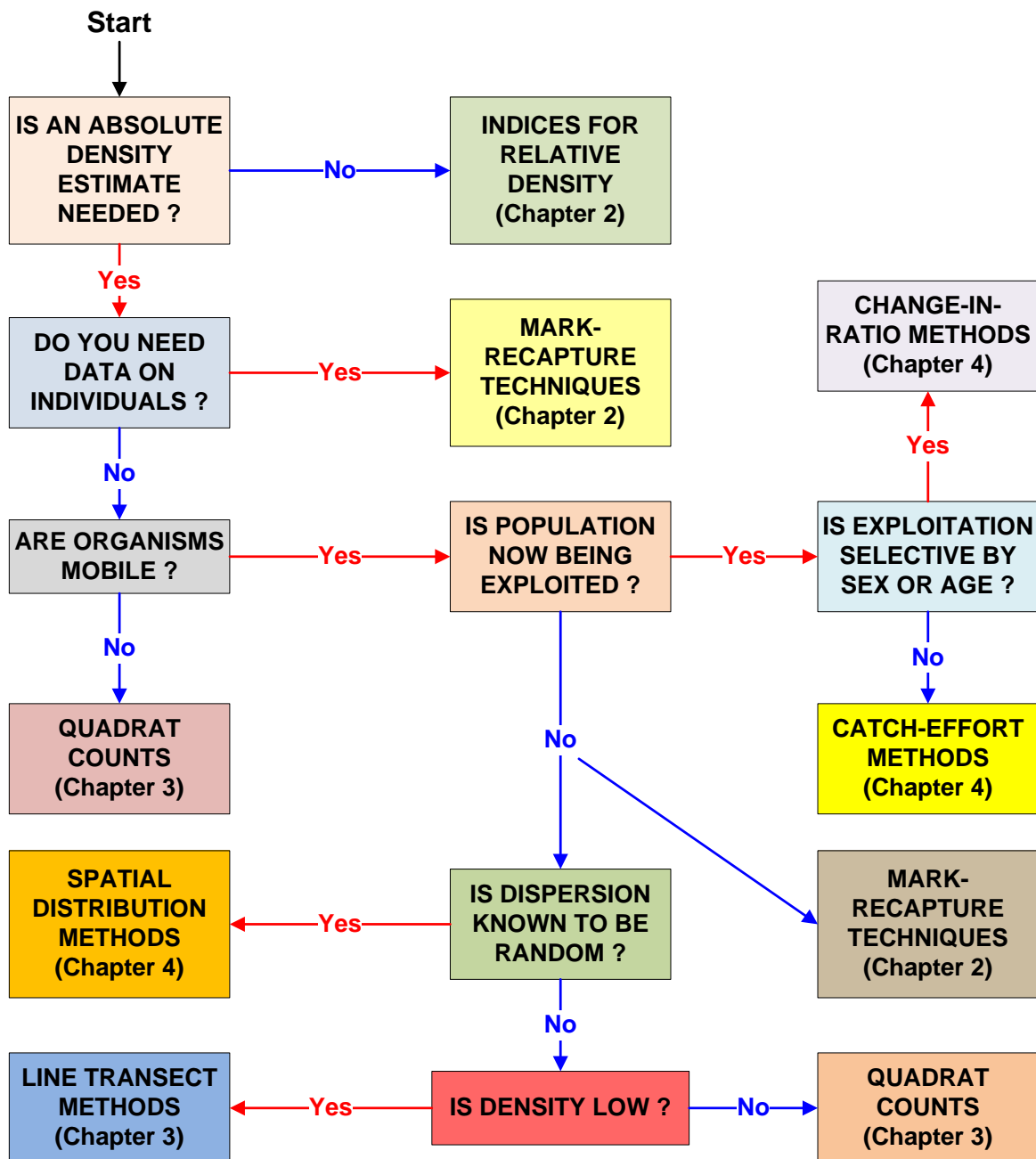


Figure A. Sequence of decisions by which a technique for estimating abundance can be chosen. (Modified from Caughley 1977.)

ESTIMATING ABUNDANCE AND DENSITY: MARK-RECAPTURE TECHNIQUES

(Version 5, 2 February 2015)

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One way to estimate the size of a population is to capture and mark individuals from the population, and then to resample to see what fraction of individuals carry marks. John Graunt first used this simple principle to estimate the human population of London in 1662. The first ecological use of mark-and-recapture was carried out by the Danish fisheries biologist C.G.J. Petersen in 1896 (Ricker 1975). Tagging of fish was first used to study movements and migration of individuals, but Petersen realized that tagging could also be used to estimate population size and to measure mortality rates. Fisheries biologists were well advanced over others in applying these methods. Lincoln (1930) used mark-recapture to estimate the abundance of ducks from band returns, and

Jackson (1933) was the first entomologist to apply mark-recapture methods to insect populations. This chapter concentrates on the mark-and-recapture techniques which are used most often when data are required on individual organisms that are highly mobile. The strength of mark-and-recapture techniques is that they can be used to provide information on birth, death, and movement rates in addition to information on absolute abundance. The weakness of these techniques is that they require considerable time and effort to get the required data and, to be accurate, they require a set of very restrictive assumptions about the properties of the population being studied. Seber (1982), Otis *et al.* (1978), Pollock *et al.* (1990) and Amstrup *et al.* (2006) have described mark-and-recapture methods in great detail, and this chapter is an abstract of the more common methods they describe.

Mark-and-recapture techniques may be used for *open* or *closed* populations. A *closed* population is one which does not change in size during the study period, that is, one in which the effects of births, deaths, and movements are negligible. Thus populations are typically closed over only a short period of time. An *open* population is the more usual case, a population changing in size and composition from births, deaths, and movements. Different methods must be applied to open and closed populations, and I will discuss five cases in this chapter:

Closed populations

1. Single marking, single recapture - *Petersen method*
2. Multiple markings and recaptures - *Schnabel method*
3. Program CAPTURE and Program MARK

Open populations

1. Multiple census – *Cormack-Jolly-Seber method*.

Robust methods

1. Combining information from closed and open methods.

2.1 PETERSEN METHOD

The Petersen method is the simplest mark-and-recapture method because it is based on a single episode of marking animals, and a second single episode of recapturing individuals. The basic procedure is to mark a number of individuals over a short time, release them, and then to recapture individuals to check for marks. All individuals can be marked in the same way. The second sample must be a *random* sample for this method to be valid; that is, all individuals must have an equal chance of being captured in the second sample, regardless of whether they are marked or not. The data obtained are

M = Number of individuals marked in the first sample

C = Total number of individuals captured in the second sample

R = Number of individuals in second sample that are marked.

From these three variables, we need to obtain an estimate of

N = Size of population at time of marking

By a proportionality argument, we obtain:

$$\frac{N}{M} = \frac{C}{R}$$

or transposing:

$$\hat{N} = \frac{C M}{R} \quad (2.1)$$

where \hat{N} = Estimate of population size at time of marking*
and the other terms are defined above.

This formula is the "Petersen estimate" of population size and has been widely used because it is intuitively clear. Unfortunately, formula (2.1) produces a *biased* estimator of population size, tending to overestimate the actual population. This bias can be large for small samples, and several formulae have been suggested to reduce this bias. Seber (1982) recommends the estimator:

$$\hat{N} = \frac{(M+1)(C+1)}{(R+1)} - 1 \quad (2.2)$$

which is unbiased if $(M + C) > N$ and nearly unbiased if there are at least seven recaptures of marked animals ($R > 7$). This formula assumes sampling *without* replacement (see page 000) in the second sample, so any individual can only be counted once.

In some ecological situations, the second sample of a Petersen series is taken *with* replacement so that a given individual can be counted more than once. For example, animals may be merely observed at the second sampling and not captured. For these cases the size of the second sample (C) can be even larger than total population size (N) because individuals might be sighted several times. In this situation we must assume that the chances of sighting a marked animal are on the average equal to the chances of sighting an unmarked animal. The appropriate estimator from Bailey (1952) is:

$$\hat{N} = \frac{M (C+1)}{(R+1)} \quad (2.3)$$

* A ^ over a variable means "an estimate of".

which differs only very slightly from equation (2.2) and is nearly unbiased when the number of recaptures (R) is 7 or more.

2.1.1 Confidence Intervals for the Petersen Method

How reliable are these estimates of population size? To answer this critical question, a statistician constructs *confidence intervals* around the estimates. A *confidence interval* is a range of values which is expected to include the true population size a given percentage of the time. Typically the given percentage is 95% but you can construct 90% or 99% confidence intervals, or any range you wish. The high and low values of a confidence interval are called the *confidence limits*. Clearly, one wants confidence intervals to be as small as possible, and the statistician's job is to recommend confidence intervals of minimal size consistent with the assumptions of the data at hand.

Confidence intervals are akin to gambling. You can state that the chances of flipping a coin and getting "heads" is 50%, but after the coin is flipped, it is either "heads" or "tails". Similarly, after you have estimated population size by the Petersen method and calculated the confidence interval, the true population size (unfortunately not known to you!) will either be inside your confidence interval or outside it. You cannot know which, and all the statistician can do is tell you that *on the average* 95% of confidence intervals will cover the true population size. Alas, you only have one estimate, and *on the average* does not tell you whether your one confidence interval is lucky or unlucky.

Confidence intervals are an important guide to the precision of your estimates. If a Petersen population estimate has a very wide confidence interval, you should not place too much faith in it. If you wish you can take a larger sample next time and narrow the confidence limits. But remember that even when the confidence interval is narrow, the true population size may *sometimes* be outside the interval. Figure 2.1 illustrates the variability of Petersen population estimates from artificial populations of known size, and shows that some random samples by chance produce confidence intervals that do not include the true value.

Several techniques of obtaining confidence intervals for Petersen estimates of population size are available, and the particular one to use for any specific set of data depends upon the size of the population in relation to the samples we have taken. Seber (1982) gives the following general guide:

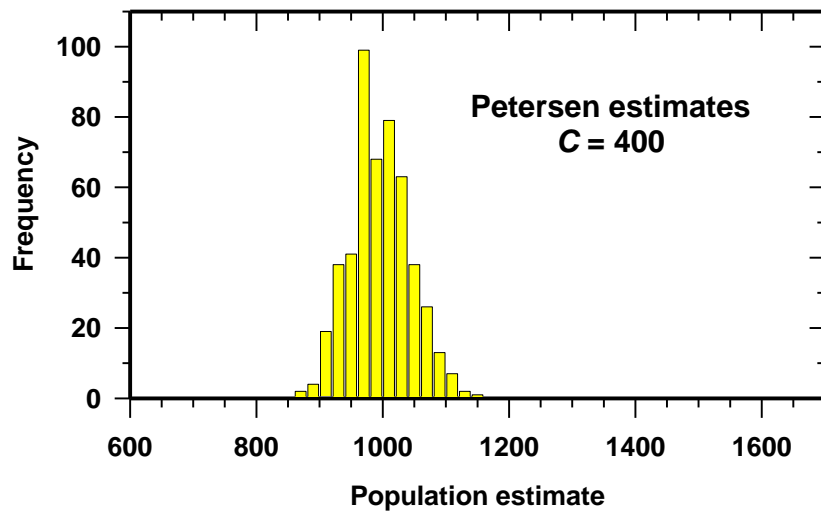
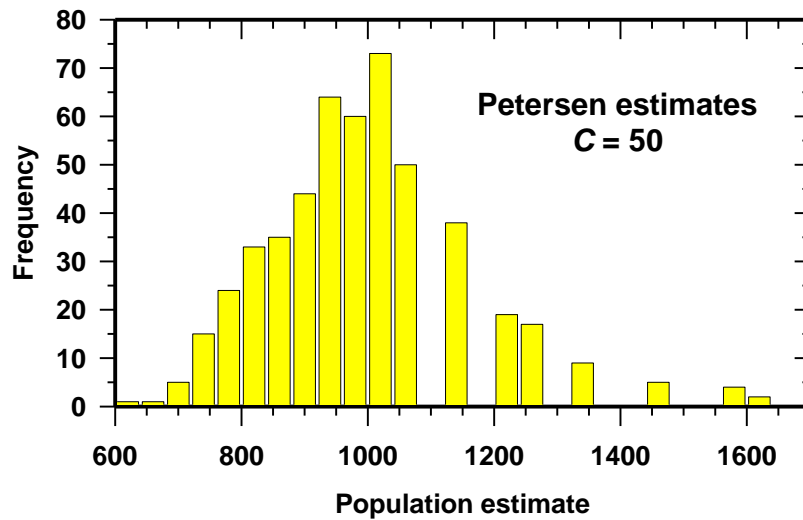
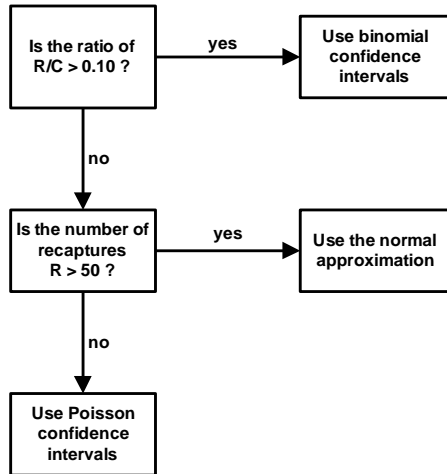


Figure 2.1 Petersen population estimates for an artificial population of $N = 1000$. Five hundred replicate samples were drawn. In both cases $M = 400$ individuals were marked in the first sample. (a) Samples of $C = 50$ were taken repeatedly for the second sample. A total of 13 estimates out of 500 did not include the known population size of 1000 (estimates below 705 or above 1570). (b) Samples of $C = 400$ were taken for the second sample. A total of 22 estimates out of 500 did not include the known population size (estimates below 910 or above 1105). Note the wide range of estimates of population size when the number of animals recaptured is small.

Poisson Confidence Intervals We discuss the Poisson distribution in detail in Chapter 4 (page 000), and we are concerned here only with the mechanics of determining confidence intervals for a Poisson variable.

Table 2.1 provides a convenient listing of values for obtaining 95% confidence intervals based on the Poisson distribution. An example will illustrate this technique. If I mark 600 (M) and then recatch a total of 200 (C) animals, 13 (R) of which are marked, from Table 2.1:

lower 95% confidence limit of R when R is 13 = 6.686

upper 95% limit of R when R is 13 = 21.364

and the 95% confidence interval for estimated population size (sampling without replacement) is obtained by using these values of R in equation (2.2):

$$\text{Lower 95\% confidence limit on } \hat{N} = \frac{(601)(201)}{21.364 + 1} - 1 = 5402$$

$$\text{Upper 95\% confidence limit on } \hat{N} = \frac{(601)(201)}{6.686 + 1} - 1 = 15,716$$

Table 2.1 Confidence limits for a Poisson frequency distribution. Given the number of organisms observed (x), this table provides the upper and lower limits from the Poisson distribution. This table cannot be used unless you are sure the observed counts are adequately described by a Poisson distribution.

95%		99%		95%		99%	
x	Lower	Upper	Lower	Upper	x	Lower	Upper
0	0	3.285	0	4.771	51	37.67	66.76
1	0.051	5.323	0.010	6.914	52	38.16	66.76
2	0.355	6.686	0.149	8.727	53	39.76	68.10
3	0.818	8.102	0.436	10.473	54	40.94	69.62

4	1.366	9.598	0.823	12.347	55	40.94	71.09	37.82	76.61
5	1.970	11.177	1.279	13.793	56	41.75	71.28	38.94	77.15
6	2.613	12.817	1.785	15.277	57	43.45	72.66	38.94	78.71
7	3.285	13.765	2.330	16.801	58	44.26	74.22	40.37	80.06
8	3.285	14.921	2.906	18.362	59	44.26	75.49	41.39	80.65
9	4.460	16.768	3.507	19.462	60	45.28	75.78	41.39	82.21
10	5.323	17.633	4.130	20.676	61	47.02	77.16	42.85	83.56
11	5.323	19.050	4.771	22.042	62	47.69	78.73	43.91	84.12
12	6.686	20.335	4.771	23.765	63	47.69	79.98	43.91	85.65
13	6.686	21.364	5.829	24.925	64	48.74	80.25	45.26	87.12
14	8.102	22.945	6.668	25.992	65	50.42	81.61	46.50	87.55
15	8.102	23.762	6.914	27.718	66	51.29	83.14	46.50	89.05
16	9.598	25.400	7.756	28.852	67	51.29	84.57	47.62	90.72
17	9.598	26.306	8.727	29.900	68	52.15	84.67	49.13	90.96
18	11.177	27.735	8.727	31.839	69	53.72	86.01	49.13	92.42
19	11.177	28.966	10.009	32.547	70	54.99	87.48	49.96	94.34
20	12.817	30.017	10.473	34.183	71	54.99	89.23	51.78	94.35
21	12.817	31.675	11.242	35.204	72	55.51	89.23	51.78	95.76
22	13.765	32.277	12.347	36.544	73	56.99	90.37	52.28	97.42
23	14.921	34.048	12.347	37.819	74	58.72	91.78	54.03	98.36
24	14.921	34.665	13.793	38.939	75	58.72	93.48	54.74	99.09
25	16.768	36.030	13.793	40.373	76	58.84	94.23	54.74	100.61
26	16.77	37.67	15.28	41.39	77	60.24	94.70	56.14	102.16
27	17.63	38.16	15.28	42.85	78	61.90	96.06	57.61	102.42
28	19.05	39.76	16.80	43.91	79	62.81	97.54	57.61	103.84
29	19.05	40.94	16.80	45.26	80	62.81	99.17	58.35	105.66
30	20.33	41.75	18.36	46.50	81	63.49	99.17	60.39	106.12
31	21.36	43.45	18.36	47.62	82	64.95	100.32	60.39	107.10
32	21.36	44.26	19.46	49.13	83	66.76	101.71	60.59	108.61
33	22.94	45.28	20.28	49.96	84	66.76	103.31	62.13	110.16
34	23.76	47.02	20.68	51.78	85	66.76	104.40	63.63	110.37

35	23.76	47.69	22.04	52.28	86	68.10	104.58	63.63	111.78
36	25.40	48.74	22.04	54.03	87	69.62	105.90	64.26	113.45
37	26.31	50.42	23.76	54.74	88	71.09	107.32	65.96	114.33
38	26.31	51.29	23.76	56.14	89	71.09	109.11	66.81	114.99
39	27.73	52.15	24.92	57.61	90	71.28	109.61	66.81	116.44
40	28.97	53.72	25.83	58.35	91	72.66	110.11	67.92	118.33
41	28.97	54.99	25.99	60.39	92	74.22	111.44	69.83	118.33
42	30.02	55.51	27.72	60.59	93	75.49	112.87	69.83	119.59
43	31.67	56.99	27.72	62.13	94	75.49	114.84	70.05	121.09
44	31.67	58.72	28.85	63.63	95	75.78	114.84	71.56	122.69
45	32.28	58.84	29.90	64.26	96	77.16	115.60	73.20	122.78
46	34.05	60.24	29.90	65.96	97	78.73	116.93	73.20	124.16
47	34.66	61.90	31.84	66.81	98	79.98	118.35	73.62	125.70
48	34.66	62.81	31.84	67.92	99	79.98	120.36	75.16	127.07
49	36.03	63.49	32.55	69.83	100	80.25	120.36	76.61	127.31
50	37.67	64.95	34.18	70.05					

Source: Crow and Gardner, 1959.

When $x > 100$ use the normal approximation:

95% confidence limits of x :

$$\text{Lower limit} = x - 0.94 - 1.96\sqrt{x - 0.02}$$

$$\text{Upper limit} = x - 1.94 - 1.96\sqrt{x - 0.98}$$

99% confidence limits of x :

$$\text{Lower limit} = x - 1.99 - 2.576\sqrt{x - 0.33}$$

$$\text{Upper limit} = x - 2.99 - 2.576\sqrt{x - 1.33}$$

Normal Approximation Confidence Intervals This method is essentially a "large sample" method which obtains a confidence interval on the fraction of marked animals in the second catch (R/C). It should be used only when R is above 50. The confidence interval for (R/C) is defined by the formula:

$$\frac{R}{C} \pm \left\{ z_{\alpha} \left[\sqrt{\frac{(1-f)(R/C)(1-R/C)}{(C-1)}} \right] + \frac{1}{2C} \right\} \quad (2.4)$$

where f = fraction of total population sampled in the second sample = R/M

$\frac{1}{2C}$ = correction for continuity

z_α = standard normal deviate for $(1-\alpha)$ level of confidence

= 1.96 (for 95% confidence limits)

= 2.576 (for 99% confidence limits)

For large samples and a large population size, both the *finite population correction* $(1-f)$ and the correction for continuity are negligible, and this formula for the normal approximation to the binomial simplifies to:

$$\frac{R}{C} \pm z_\alpha \sqrt{\frac{(R/C)(1-R/C)}{(C-1)}} \quad (2.5)$$

The constant z_α defines 100 $(1-\alpha)$ percent confidence limits, and values can be substituted from tables of the standard normal distribution (z) (e.g. Zar 1996, pg. 19). For example, for 80% confidence limits replace z_α with the constant 1.2816.

One example will illustrate this method. If I mark 1800 animals (M) and catch at the second sampling a total of 800 (C), of which 73 (R) are already tagged, from formula (2.4) for 95% confidence limits:

$$\begin{aligned} \frac{73}{800} \pm \left\{ 1.96 \left[\sqrt{\frac{(1-73/1800)(73/800)(1-73/800)}{(800-1)}} \right] + \frac{1}{2(800)} \right\} \\ = 0.09125 \pm 0.020176 \end{aligned}$$

and the 95% confidence interval for (R/C) is 0.07107 to 0.111426. To obtain a 95% confidence interval for the estimated population size we use these limits for R/C in equation (2.1):

$$\hat{N} = \frac{C M}{R}$$

$$\text{Lower 95\% confidence limit on } \hat{N} = \frac{1}{0.111426} (1800) = 16,154$$

$$\text{Upper 95\% confidence limit on } \hat{N} = \frac{1}{0.07107} (1800) = 25,326$$

Binomial Confidence Intervals Binomial confidence intervals for the fraction of marked animals (R/C) can be obtained most easily graphically from Figure 2.2. The resulting confidence interval will be approximate but should be adequate for most

ecological data. For example, suppose I mark 50 birds (M), and then capture 22 (C) birds of which 14 (R) are marked. The fraction of marked animals (R/C) is 14/22 or 0.64. Move along the X-axis (*Sample Proportion*) to 0.64, and then move up until you intercept the first sample size line of C , or 22. Then read across to the Y-axis (*Population Proportion*) to obtain 0.40, the lower 95% confidence limit for (R/C). Now repeat the procedure to intercept the second sample size line of C , or 22. Reading across again, you find on the Y-axis 0.83, the upper 95% confidence limit for (R/C).

These confidence limits can be converted to confidence limits for population size (N) by the use of these limits for (R/C) in formula (2.1), exactly as described above (page 31). We use these limits for R/C in equation (2.1):

$$\hat{N} = \frac{C M}{R}$$

$$\text{Lower 95\% confidence limit on } \hat{N} = \frac{1}{0.83}(50) = 60$$

$$\text{Upper 95\% confidence limit on } \hat{N} = \frac{1}{0.40}(50) = 125$$

Binomial 95% Confidence Limits

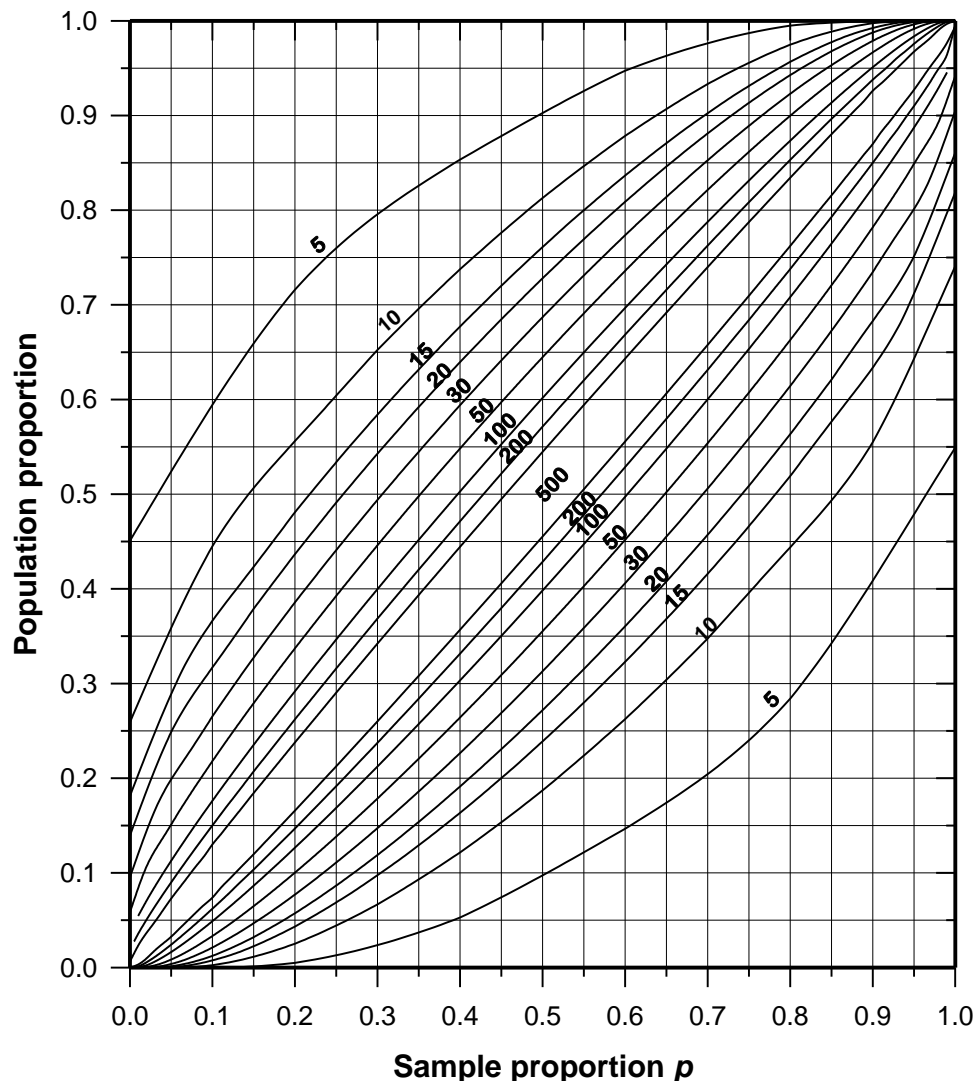


Figure 2.2 Upper and lower 95% confidence limits for a population proportion. Confidence limits are read off the y-axis for an observed value of p on the x-axis. Sample sizes are marked on the contour lines.

Alternatively and more simply, binomial confidence limits can be calculated using Program EXTRAS (Appendix 2, page 000) which uses the formulae given in Zar (1996, p. 524). For the bird example above, the tables provide the exact 95% confidence limits of 0.407 to 0.828, compared with the slightly less accurate 0.40 to 0.83 read off Figure 2.2 visually.

Program RECAP (Appendix 2, page 000) computes the Petersen estimate of population size and the appropriate confidence interval according to the

recommendations of Seber (1982). Box 2.1 illustrates how the Petersen calculations are done.

Box 2.1 PETERSEN METHOD OF POPULATION ESTIMATION

Green and Evans (1940) estimated the size of a snowshoe hare population at Lake Alexander, Minnesota, in the winter of 1932-33 from these live-trapping data (sampling without replacement):

$M = 948$ hares caught and tagged in first sample

$C = 421$ total caught in second sample

$R = 167$ marked hares in second sample

Biased Estimator (equation 2.1)

$$\begin{aligned}\hat{N} &= \frac{CM}{R} \\ &= \frac{(421)(948)}{167} = 2390 \text{ hares}\end{aligned}$$

Unbiased Estimator (equation 2.2)

$$\begin{aligned}\hat{N} &= \frac{(M+1)(C+1)}{(R+1)} - 1 \\ &= \frac{(421+1)(948+1)}{167+1} - 1 = 2383 \text{ hares}\end{aligned}$$

Confidence Interval

$R/C = 0.3967$ so we use a binomial confidence interval. We can read the approximate confidence limits off Figure 2.2, and this provides visual estimates of 0.35 to 0.45 as 95% confidence limits.

We thus obtain a confidence interval for population size as:

$$\text{Lower 95\% confidence limit on } \hat{N} = \frac{C}{R} M = \frac{1}{0.45} (948) = 2107$$

$$\text{Upper 95\% confidence limit on } \hat{N} = \frac{C}{R} M = \frac{1}{0.35} (948) = 2709$$

If we use the more exact equations for binomial confidence limits given by Zar (1996, p. 524) we obtain 95% confidence limits of 0.369 to 0.425 for the ratio of

R/C, and narrower confidence limits of 2231 to 2569 individuals.

These calculations can be done in Program RECAP (Appendix 2, page 000)

2.1.2 Sample Size Needed for Petersen Estimates

Let us now turn the Petersen method upside down and ask, given a rough estimate of population size (*N*), *how large a sample do I need to take* to get a good estimate of abundance. This is a key question for a great deal of ecological work that uses mark-recapture techniques, and should be asked *before* a study is done, not afterward. Two preliminary bits of information must be given before an answer to the sample size question can be given precisely:

1. Initial estimate of population size (*N*)
2. Accuracy desired in Petersen estimate

The first requirement is the usual statistical one of "knowing the answer before you do any of the work", but this can be a very rough, order-of-magnitude guess. The only rule is to guess on the high side if you wish to be conservative.

The second requirement needs a quantitative definition of *accuracy*. We desire our estimate of population size to be within a certain range of the true value, and we call this the accuracy (*A*):

$$A = \pm 100 \left(\frac{\text{Estimated population size} - \text{true population size}}{\text{True population size}} \right)$$

where *A* = accuracy of an estimate (as a percentage)

Thus we may wish our estimate to be within $\pm 10\%$ accuracy. We cannot guarantee this accuracy all the time, and we must allow a probability (α) of not achieving our desired accuracy. Robson and Regier (1964) suggest using an α of 0.05 and three standard levels for *A*:

1. *Preliminary surveys*: $A = \pm 50\%$; in these cases only a rough idea of population size is needed.
2. *Management work*: $A = \pm 25\%$; a moderate level of accuracy is desired.
3. *Research work*: $A = \pm 10\%$; in these cases quite accurate data on population size is required.

Figure 2.3 gives sample sizes needed for small populations for the three levels of accuracy, and Figure 2.4 gives sample sizes needed for large populations. Both these graphs are to be read in the same way. The "contour lines" on the graph are estimated population sizes (N). The vertical and horizontal axes of the graphs are values of M , number marked in the first Petersen sample, and C , number caught in the second Petersen sample. From the contour line corresponding to your estimated population size, read off pairs of M , C values. All of these pairs of values are suitable for obtaining the accuracy specified, and you can pick any set which you like.

EXAMPLE 1

$A = \pm 25\%$, rough population estimate, $\hat{N} = 20$; reading from the contour line of

M	C	
1	20	Any one of these four pairs will produce the desired accuracy
10	15	
15	10	
17	8	

$N = 20$ in Figure 2.3(b):

EXAMPLE 2

$A = \pm 10\%$, rough estimate $\hat{N} = 200,000$; reading from the contour line of $N =$

M	C	
125,000	200	Any one of these four pairs will produce the desired accuracy
92,000	400	
30,000	2000	
7,000	10,000	

200,000 in Figure 2.4(c):

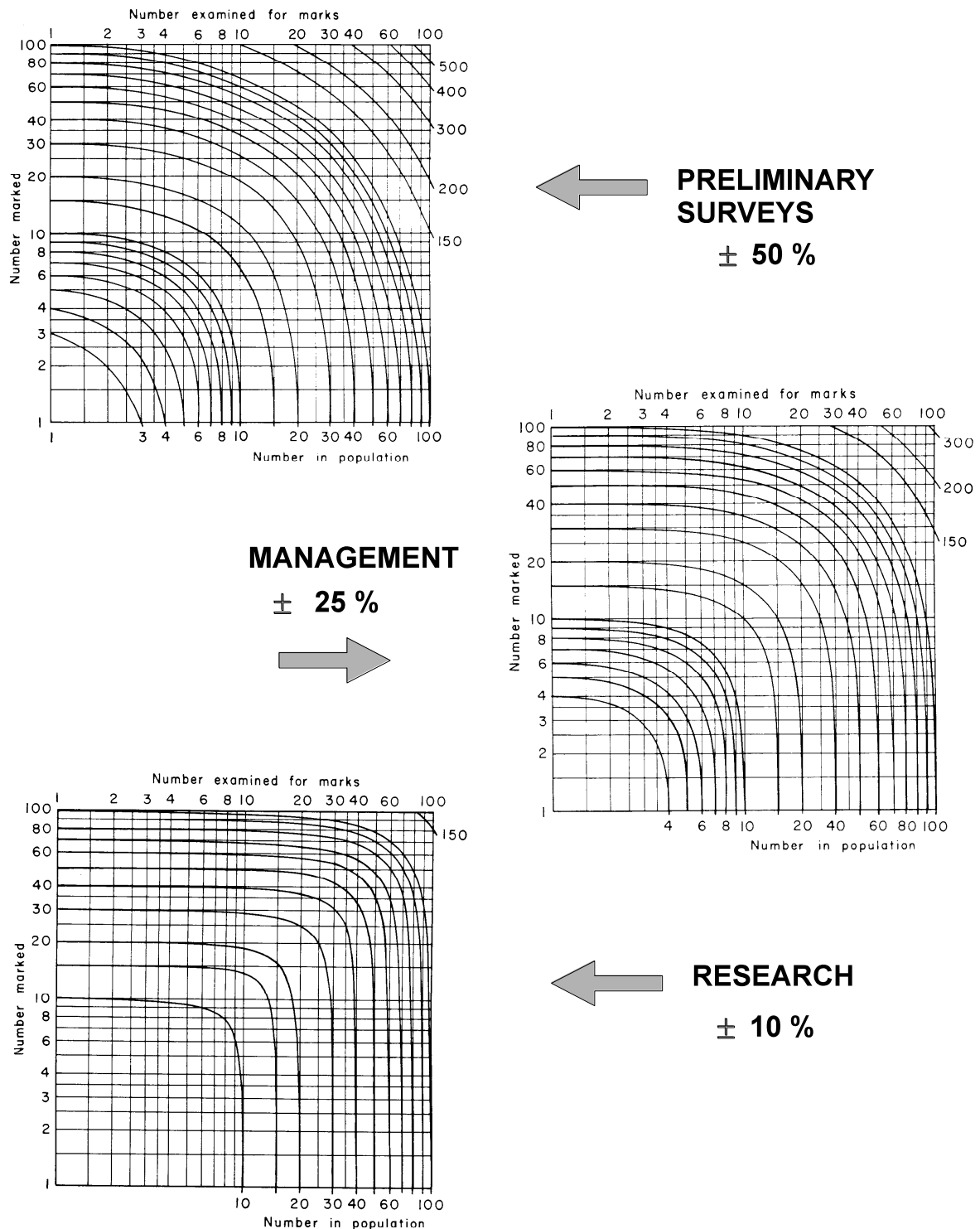


Figure 2.3 Sample size charts for Petersen population estimates for *small* populations. α is 5% in all cases. For preliminary surveys an accuracy of $\pm 50\%$ is recommended, for management studies $\pm 25\%$, and for research $\pm 10\%$. (After Robson and Regier 1964.)

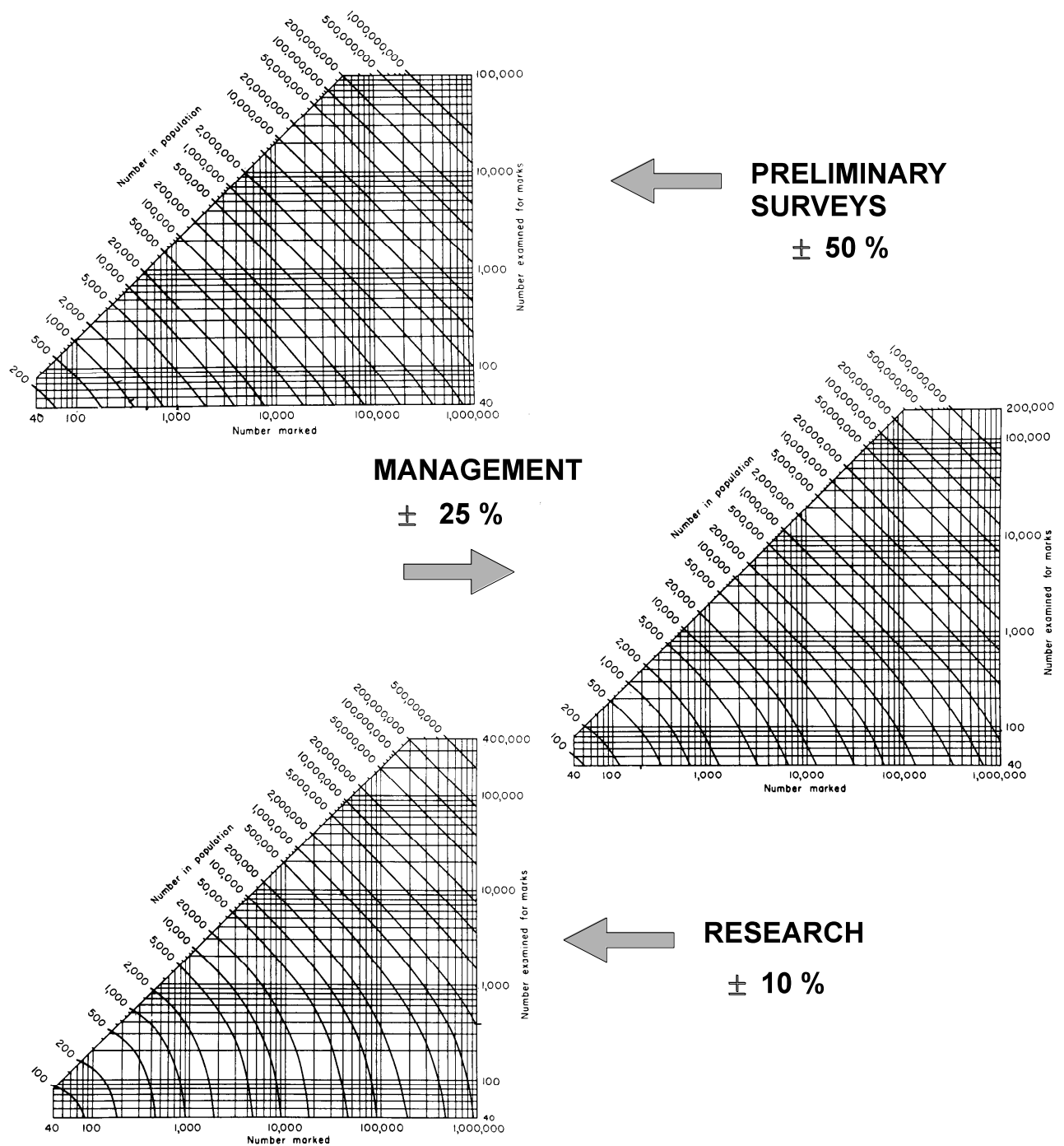


Figure 2.4 Sample size charts for Petersen population estimates for *large* populations. α is 5% in all cases. For preliminary surveys an accuracy of $\pm 50\%$ is recommended, for management studies $\pm 25\%$, and for research $\pm 10\%$. These charts are a continuation of those in Figure 2.3. (After Robson and Regier 1964.)

The choice of which combination of marking (M) and capturing (C) will depend in part on the ease of marking and ease of sampling for marked individuals. For example, it may be very easy to mark individuals, but very difficult to recapture large samples. In this situation in example 2 we might decide to take $M = 92,000$ and $C = 400$. Alternatively, it may be very expensive to mark animals and cheap to recapture them in large numbers, and we might take $M = 7000$ and $C = 10,000$ for the same example. In normal circumstances we try to equalize sample sizes so $M \approx C$, the number marked is approximately the same as the number caught in the second Petersen sample. This balance of $M \approx C$ is the point of minimum effort in terms of numbers of animals that need to be handled to achieve a given level of precision.

I cannot overemphasize the importance of going through this sample size estimation procedure *before you start* an ecological study which uses mark-recapture. To obtain even moderate accuracy in population estimation it is often necessary to mark 50% or more of the individuals in a population and the information you can obtain from Figures 2.3 and 2.4 can tell you how much work you must do and whether the project you are starting is feasible at all.

2.1.3 Assumptions of Petersen Method

For \hat{N} in formula (2.2) or (2.3) to be an accurate estimate of population size the following five assumptions must hold:

1. The population is *closed*, so that N is constant.
2. All animals have the same chance of getting caught in the first sample.
3. Marking individuals does not affect their catchability.
4. Animals do not lose marks between the two sampling periods.
5. All marks are reported upon discovery in the second sample.

If the first assumption is to hold in a biological population, it is essential that the Petersen method be applied over a short period of time. This is an important consideration in experimental design because if a long period of sampling is needed to get the size of sample required, the method may lose its precision.

There are several simple ways in which the first assumption can be violated without affecting the validity of the Petersen estimate. If there are accidental deaths during the first sampling and marking, the estimate of N is valid but refers to the number of individuals *alive* in the population after the first sample is released. Natural mortality may occur between the first and second Petersen samples without affecting the estimation if marked and unmarked animals have an equal chance of dying between the first and second samples. The question of whether mortality falls equally on marked and unmarked animals is difficult to answer for any natural population, and this assumption is best avoided if possible.

Population size (N) in a mark-recapture estimation always refers to the *catchable population*, which may or may not be the entire population. For example, nets will catch only fish above a certain size, and smaller individuals are thus ignored in the Petersen calculations. The recruitment of young animals into the catchable population between the first and second samples tends to decrease the proportion of marked animals in the second sample and thus inflate the Petersen estimate of N above the true population size at time one. When there is recruitment but no mortality, \hat{N} will be a valid estimate of population size at the time of the second sample. Fishery scientists have developed tests for recruitment and subsequent corrections that can be applied to Petersen estimates when there is recruitment (see Seber (1982), p. 72 ff.), but the best advice is still the simplest: avoid recruitment of new individuals into the population by sampling over a short time interval.

One of the crucial assumptions of mark-recapture work is that marked and unmarked animals are equally catchable. This assumption is necessary for all the methods discussed in this chapter and I defer discussion until later (page 000) on methods for testing this assumption.

Random sampling is critical if we are to obtain accurate Petersen estimates, but it is difficult to achieve in field programs. We cannot number all the animals in the population and select randomly M individuals for marking and later C individuals for capture. If all animals are equally catchable, we can approximate a random sample by sampling *areas* at random with a constant effort. We can divide the total area into equal subareas, and allot sampling effort to the subareas selected from a random number table. All points selected must be sampled with the same effort.

Systematic sampling (Chapter 8, page 000) is often used in place of random sampling. Systematic sampling will provide adequate estimates of population size only if there is uniform mixing of marked and unmarked animals, and all individuals are equally catchable. Uniform mixing is unlikely to be achieved in most animals which show territorial behavior or well-defined home ranges. Where possible you should aim for a random sample and avoid the dangerous assumption of uniform mixing that must be made after systematic samples are taken.

I will not review here the various marking methods applied to animals and plants. Seber (1982) and Sutherland (2006) give general references for marking methods for fish, birds, mammals, and insects. Experienced field workers can offer much practical advice on marking specific kinds of organisms, and not all of this advice is contained in books. New metals, plastics, and dyes are constantly being developed as well. The importance of these technological developments in marking cannot be overemphasized because of the problems of lost marks and unreported marks. Poor marking techniques

will destroy the most carefully designed and statistically perfect mark-recapture scheme, and it is important to use durable tags that will not interfere with the animal's life cycle.

Tag losses can be estimated easily by giving all the M individuals in the first Petersen sample two types of tags, and then by recording in the second sample:

R_A = number of tagged animals in second sample with only an A type tag
(i.e. they have lost their B-tag)

R_B = number of tagged animals in second sample with only a B type tag
(i.e. they have lost their A-tag)

R_{AB} = number of tagged animals in second sample with both A and B tags present.

Clearly, if R_A and R_B are both zero you are probably not having a tag loss problem. The total number of recaptures is defined as

$$R = R_A + R_B + R_{AB} + \left\{ \begin{array}{l} \text{Number of individuals losing both tags} \\ \text{and thus being classed as unmarked} \end{array} \right\}$$

Seber (1982, p. 95) shows that, if we define:

$$k = \frac{R_A R_B}{(R_A + R_{AB})(R_B + R_{AB})}$$

and

$$c = \frac{1}{1-k}$$

Then we can estimate the total number of recaptures as:

$$\hat{R} = c(R_A + R_B + R_{AB}) \quad (2.6)$$

For example, if we mark 500 beetles with dots of cellulose paint (A) and reflecting paint (B) and obtain in the second sample:

$$R_A = 23$$

$$R_B = 6$$

$$R_{AB} = 127$$

we obtain:

$$k = \frac{(23)(6)}{(23+127)(6+127)} = 0.006917$$

$$c = \frac{1}{1 - 0.006917} = 1.00697$$

$$\hat{R} = 1.00697 (23 + 6 + 127) = 157.09$$

Thus we observe $R = 156$ and estimate $\hat{R} = 157$ so that only one insect is estimated to have lost both marks during the experiment. From this type of experiment we can calculate the probabilities of losing marks of a given type:

$$\left\{ \begin{array}{l} \text{Probability of losing a tag of Type A} \\ \text{between samples one and two} \end{array} \right\} = \frac{R_B}{(R_B + R_{AB})} \quad (2.7)$$

$$\left\{ \begin{array}{l} \text{Probability of losing a tag of Type B} \\ \text{between samples one and two} \end{array} \right\} = \frac{R_A}{(R_A + R_{AB})} \quad (2.8)$$

In this example the probability of losing a cellulose dot is only 0.045 but the chances of losing a reflecting dot are 0.153, more than a three-fold difference between tag types.

The failure to report all tags recovered may be important for species sampled by hunting or commercial fishing in which the individuals recovering the tags are not particularly interested in the data obtained. Tag returns are affected by the size of the tag reward and the ease of visibility of the tags.

An array of radio- and satellite-collar methods can estimate tag loss for collars directly. Musyl et al. (2011) have an excellent discussion of problems of satellite tag loss in fishes and sea turtles and the statistical methods that can be used to deal with tag loss estimation.

2.2 SCHNABEL METHOD

Schnabel (1938) extended the Petersen method to a series of samples in which there is a 2nd, 3rd, 4th...nth sample. Individuals caught at each sample are first examined for marks, then marked and released. Marking occurs in each of the sampling times. Only a single type of mark need be used, since throughout a Schnabel experiment we need to distinguish only two types of individuals: *marked* = caught in one or more prior samples; and *unmarked* = never caught before. We determine for each sample t :

C_t = total number of individuals caught in sample t

R_t = number of individuals already marked when caught in sample t

U_t = number of individuals marked for first time and released in sample t

Normally $C_t = R_t + U_t$

but if there are accidental deaths involving either marked or unmarked animals, these

are subtracted from the U_t value*. The number of marked individuals in the population continues to accumulate as we add further samples, and we define:

$$M_t = \left\{ \begin{array}{l} \text{number of marked individuals in the population} \\ \text{just before the } t\text{-th sample is taken} \end{array} \right\}$$

$$M_t = \sum_{i=1}^{t-1} U_i$$

so that, for example, $M_6 = U_1 + U_2 + U_3 + U_4 + U_5$

Table 2.2 gives an example of some Schnabel-type data obtained on a sunfish population.

Given these counts of marked and unmarked individuals, we need to derive an estimate of population size N for a closed population. Ricker (1975) gives several methods, and Seber (1982, Chap. 4) discusses this estimation problem in detail. We will describe here two methods of estimation, the original Schnabel method and the Schumacher and Eschmeyer method, which is the most robust and useful ecological model according to Seber (1982).

Schnabel Method: Schnabel (1938) treats the multiple samples as a series of Petersen samples and she obtained a population estimate as a weighted average of Petersen estimates:

$$\hat{N} = \frac{\sum_t (C_t M_t)}{\sum_t R_t} \quad (2.9)$$

If the fraction of the total population that is caught in each sample (C_t/\hat{N}) and the fraction of the total population that is marked (M_t/\hat{N}) is always less than 0.1, a better estimate is:

$$\hat{N} = \frac{\sum_t (C_t M_t)}{\sum_t R_t + 1} \quad (2.10)$$

The variance of the Schnabel estimator is calculated on the reciprocal of N :

* The number of accidental deaths is assumed to be small.

$$\text{Variance} \left(\frac{1}{\hat{N}} \right) = \frac{\sum R_t}{\left(\sum C_t M_t \right)^2} \quad (2.11)$$

$$\text{Standard Error of } \frac{1}{\hat{N}} = \sqrt{\text{Variance} \left(\frac{1}{\hat{N}} \right)} \quad (2.12)$$

Schumacher and Eschmeyer Method: Schumacher and Eschmeyer (1943) pointed out that if one plotted on arithmetic paper:

X-axis: M_t , number of individuals previously marked (before time t)

Y-axis: R_t/C_t , proportion of marked individuals in the t -th sample

the plotted points should lie on a straight line of slope $(1/N)$ passing through the origin. Thus one could use linear regression techniques to obtain an estimate of the slope $(1/N)$ and thus an estimate of population size. The appropriate formula of estimation is:

$$\hat{N} = \frac{\sum_{t=1}^s (C_t M_t^2)}{\sum_{t=1}^s (R_t M_t)} \quad (2.13)$$

where s = total number of samples

The variance of Schumacher estimator is obtained from linear regression theory as the variance of the slope of the regression (Zar 1996, p. 330; Sokal and Rohlf 1995, p. 471). In terms of mark-recapture data:

$$\text{Variance of} \left(\frac{1}{\hat{N}} \right) = \frac{\sum \left(R_t^2 / C_t \right) - \left[\left(\sum R_t M_t \right)^2 / \sum C_t M_t^2 \right]}{s-2} \quad (2.14)$$

where s = number of samples included in the summations

The standard error of the slope of the regression is obtained as follows:

$$\text{Standard Error of} \left(\frac{1}{\hat{N}} \right) = \sqrt{\frac{\text{Variance of} \left(\frac{1}{\hat{N}} \right)}{\sum (C_t M_t^2)}} \quad (2.15)$$

2.2.1 Confidence Intervals for Schnabel Estimates

If the total number of recaptures ($\sum R_t$) is less than 50, confidence limits for the Schnabel population estimate should be obtained from the Poisson distribution (Table

2.1, page 30). These confidence limits for $\sum R_t$ from Table 2.1 can be substituted into equations (2.14) or (2.15) as the denominator, and the upper and lower confidence limits for population size estimated.

For the Schnabel method if the total number of recaptures ($\sum R_t$) is above 50, use the normal approximation derived by Seber (1982, p. 142). This large-sample procedure uses the standard error and a t -table to get confidence limits for $\left(\frac{1}{\hat{N}}\right)$ as follows:

$$\frac{1}{\hat{N}} \pm t_{\alpha} \text{ S.E.} \quad (2.16)$$

where S.E. = standard error of $1/N$ (equation 2.12 or 2.15)

t_{α} = value from Student's t -table for $(100 - \alpha)\%$ confidence limits.

Enter the t -table with $(s-1)$ degrees of freedom for the Schnabel method and $(s-2)$ degrees of freedom for the Schumacher and Eschmeyer methods, where s is the number of samples. Invert these limits to obtain confidence limits for \hat{N} . Note that this method (equation 2.16) is used for all Schumacher-Eschmeyer estimates, regardless of the number of recaptures. This procedure is an approximation but the confidence limits obtained are sufficiently accurate for all practical purposes.

We can use the data in Table 2.2 to illustrate both these calculations. From the data in Table 2.2 we obtain:

TABLE 2.2 Mark-recapture data obtained for a Schnabel-type estimate of population size

Date, t	Number of fish caught C_t	Number of recaptures ^b R_t	Number newly marked (less deaths) ^c	Marked fish at large ^d M_t
June 2	10	0	10	0
June 3	27	0	27	10
June 4	17	0	17	37
June 5	7	0	7	54
June 6	1	0	1	61
June 7	5	0	5	62
June 8	6	2	4	67
June 9	15	1	14	71
June 10	9	5	4	85
June 11	18	5	13	89
June 12	16	4	10	102
June 13	5	2	3	112
June 14	7	2	4	115
June 15	19	3	-	119
Totals	162	24	119	984

^a S.D. Gerking (1953) marked and released sunfish in an Indiana lake for 14 days and obtained these data.

^b The number of fish already marked when taken from the nets.

^c Note that there were two accidental deaths on June 12 and one death on June 14.

^d Number of marked fish assumed to be alive in the lake in the instant just before sample t is taken.

$$\sum C_t M_t = 10,740$$

$$\sum (C_t M_t^2) = 970,296$$

$$\sum R_t M_t = 2294$$

$$\sum \left(\frac{R_t^2}{C_t} \right) = 7.7452$$

For the Schnabel estimator, from equation (2.9)

$$\hat{N} = \frac{10,740}{24} = 447.5 \text{ sunfish}$$

A 95% confidence interval for this estimate is obtained from the Poisson distribution because there are only 24 recaptures. From Table 2.1 with $\sum R_t = 24$ recaptures, the 95% confidence limits on $\sum R_t$ are 14.921 and 34.665. Using equation (2.9) with these limits we obtain:

$$\text{Lower 95\% confidence limit} = \frac{\sum (C_t M_t)}{\sum R_t} = \frac{10,740}{34.665} = 309.8$$

$$\text{Upper 95\% confidence limit} = \frac{\sum (C_t M_t)}{\sum R_t} = \frac{10,740}{14.921} = 719.8 \text{ sunfish}$$

The 95% confidence limits for the Schnabel population estimate are 310 to 720 for the data in Table 2.1.

For the Schumacher-Eschmeyer estimator, from equation (2.13):

$$\hat{N} = \frac{970,296}{2294} = 423 \text{ sunfish}$$

The variance of this estimate, from equation (2.14), is:

$$\text{Variance of } \left(\frac{1}{\hat{N}} \right) = \frac{7.7452 - \left[\frac{(2294)^2}{970,296} \right]}{14 - 2} = 0.1934719$$

$$\text{Standard error } \left(\frac{1}{\hat{N}} \right) = \sqrt{\frac{0.1934719}{970,296}} = 0.0004465364$$

The confidence interval from equation (2.16) is:

$$\frac{1}{423} \pm (2.179)(0.0004465364)$$

or 0.0013912 to 0.0033372. Taking reciprocals, the 95% confidence limits for the Schumacher-Eschmeyer estimator are 300 and 719 sunfish, very similar to those obtained from the Schnable method.

Seber (1982) recommends the Schumacher-Eschmeyer estimator as the most robust and useful one for multiple censuses on closed populations. Program RECAP (Appendix 2, page 000) computes both these estimates and their appropriate confidence intervals. Box 2.2 illustrates an example of the use of the Schumacher-Eschmeyer estimator.

Box 2.2 Schnabel Method of Population Estimation

Turner (1960) obtained data on a frog population sampled over 5 days:

Sample #	No. caught C_t	No. recaptures R_t	No. newly marked (less deaths)	No. marked frogs at large M_t
1	32	0	32	0
2	54	18	36	32
3	37	31	6	68
4	60	47	13	74
5	41	36	5	87

$$\sum C_t M_t^2 = (32)(0^2) + (54)(32^2) + \dots + (41)(87^2) = 865,273$$

$$\sum R_t M_t = (0)(0) + (18)(32) + \dots + (36)(87) = 9294$$

$$\sum \frac{R_t^2}{C_t} = \frac{(18)^2}{54} + \frac{(31)^2}{37} + \dots = 100.3994$$

To estimate population size using the Schumacher-Eschmeyer method, we obtain from equation (2.13):

$$\hat{N} = \frac{\sum_{t=1}^s (C_t M_t^2)}{\sum_{t=1}^s (R_t M_t)} = \frac{865,273}{9294} = 93.1 \text{ frogs}$$

To obtain confidence intervals, we can use the normal approximation method defined

in equations (2.14) and (2.15) as follows:

$$\text{Variance of } \left(\frac{1}{\hat{N}} \right) = \frac{\sum \left(\frac{R_t^2}{C_t} \right) - \left[\frac{(\sum R_t M_t)^2}{\sum C_t M_t^2} \right]}{s-2}$$

$$\text{Variance of } \left(\frac{1}{\hat{N}} \right) = \frac{100.3994 - \left[\frac{(9294)^2}{865,273} \right]}{5-2} = 0.1904809$$

$$\text{Standard Error of } \left(\frac{1}{\hat{N}} \right) = \sqrt{\frac{\text{Variance of } \left(\frac{1}{\hat{N}} \right)}{\sum (C_t M_t^2)}}$$

$$\text{Standard Error of } \left(\frac{1}{\hat{N}} \right) = \sqrt{\frac{0.1904809}{865,273}} = 0.0004692$$

Note that it is important to maintain an excessive number of decimal places in these intermediate calculations to preserve accuracy in the final estimates.

The 95% confidence interval is, from equation (2.16):

$$\frac{1}{\hat{N}} \pm t_{\alpha} \text{ S.E.}$$

since $t_{0.025}$ for 3 d.f. = 3.182, we obtain:

$$\frac{1}{93.1} \pm (3.182)(0.0004692)$$

or 0.09248 to 0.012234. Taking reciprocals, we obtain the 95% confidence limits on population size of 82 to 108. Note that these confidence limits are *not* symmetrical about \hat{N} .

These calculations can be done by Program RECAP (Appendix 2).

2.2.2 Assumptions of the Schnabel Method

The Schnabel method makes all the same assumptions that the Petersen method makes (page 39) - that the population size is constant without recruitment or losses, that sampling is random, and all individuals have an equal chance of capture in any given

sample. Our previous discussion of the limitations these assumptions impose are thus all relevant here.

The major advantage of the multiple sampling in a Schnabel experiment is that it is easier to pick up violations of these assumptions. A regression plot of proportion of marked animals (Y) on number previously marked (X) will be linear if these assumptions are true, but will become curved when the assumptions are violated. Figure 2.5 illustrates one data set from cricket frogs which fits the expected straight line and a second data set from red-backed voles which is curvilinear. Unfortunately, there is no unique interpretation possible for curvilinear plots, and they signal that one or more assumptions are violated without telling us which assumption or how it is violated. For example, the downward curve in Figure 2.5(b) could be due to the immigration of unmarked animals into the study area, or to the fact that marked voles are less easily caught in live traps than unmarked voles.

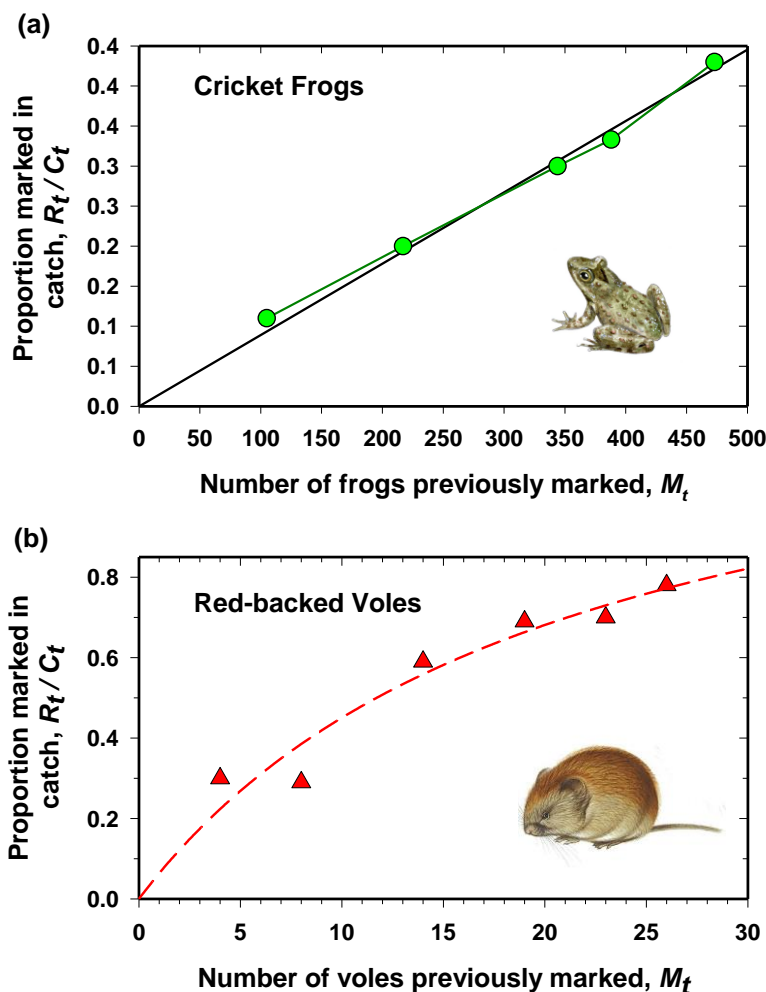


Figure 2.5 Schnabel method of population estimation: (a) cricket frogs; (b) red-backed voles. A plot of the accumulated number of marked animals (M_t) against the proportion of marked

animals in each sample (R_t/C_t) will be linear (a) if the assumptions underlying the method are fulfilled. A curvilinear plot (b) shows that the assumptions are violated and either the population is not closed or catchability is not constant. (Data from Pyburn 1958 for (a) and from Tanaka 1951 for (b)).

When a curvilinear relationship is present, you may still be able to obtain a population estimate by the use of *Tanaka's model* (see Seber, 1982, p. 145). The procedure is to plot on log-log paper:

X-axis: M_t (number marked at large)

Y-axis: C_t/R_t (number caught / number of recaptures)

Figure 2.6 shows this graph for the same vole data plotted in Figure 2.5(b).

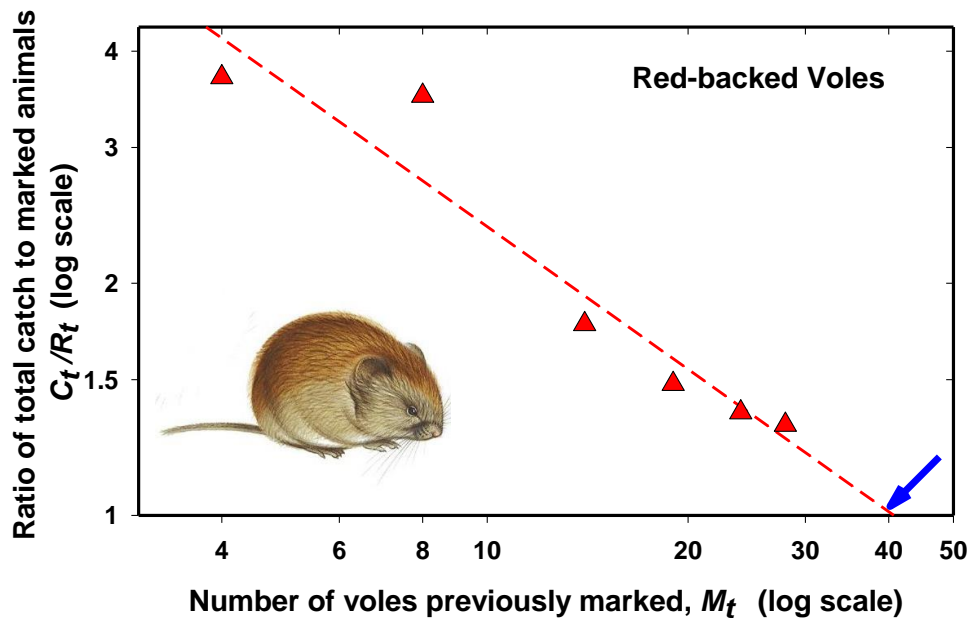


Figure 2.6 Tanaka's model of population estimation: red-backed voles. A log-log plot of the number of marked animals at large (M_t) against the ratio of total catch to marked catch (C_t/R_t) should be a straight line to fit this model, and the x-intercept (arrow) is the estimate of population size. These data are the same as those plotted in Figure 2.5b. (Data from Tanaka 1951.)

If Tanaka's model is applicable, this log-log plot should be a straight line, and the X-intercept is an estimate of population size. Thus, as a first approximation a visual estimate of N can be made by drawing the regression line by eye and obtaining the X-axis intercept, as shown in Figure 2.6. The actual formulae for calculating \hat{N} by the Tanaka method are given in Seber (1982, p. 147) and are not repeated here.

The Schnabel and Tanaka methods both assume that the number of accidental deaths or removals is negligible so that population size is constant. If a substantial fraction of the samples is removed from the population, for example by hunting or commercial fishing, corrections to the population estimates given above should be applied. Seber (1982, p. 152) provides details of how to correct these estimates for known removals.

2.3 PROGRAM CAPTURE AND PROGRAM MARK

The simple approaches to estimating population size typified by the Petersen and Schnabel methods have been superseded by more complex methods that are computer intensive. I have detailed the procedures in the Petersen and Schnabel methods to introduce you to some of the problems of estimation with mark-recapture data. In reality if you wish to use these methods you must utilize Program CAPTURE (Otis et al. 1978) or Program MARK (White 2008, Cooch and White 2010). We begin with Program CAPTURE.

Simple models for closed populations like the Petersen Method may fail because of two assumptions that are critical for estimation:

1. All animals have the same chance of getting caught in all the samples.
2. Marking individuals does not affect their catchability in later samples

Otis et al. (1978) set out an array of models in Program CAPTURE that take into account some of the simpler aspects of unequal catchability. These methods complement the Petersen and Schnabel estimators discussed above for closed populations but they are more restrictive because all the methods in Program CAPTURE assume that every marked animal can be individually recognized and at least three sampling periods were used. These methods are all computer-intensive¹. They involve more complex mathematics than we can discuss here in detail and I will cover 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 for 7 capture times is as follows:

¹ These programs are currently available from Colorado State University at www.cnr.colostate.edu/~gwhite/software.html.

Tag number	Time 1	Time 2	Time 3	Time 4	Time5	Time 6	Time 7
3455	1	0	0	1	1	1	0
3456	1	1	1	0	0	0	1
3458	1	0	0	0	0	0	0
3462	0	1	1	1	1	0	0
3463	0	0	0	1	0	1	0
3476	0	0	1	0	1	0	1
3488	0	0	0	0	0	0	1

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 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 the analog of the Petersen and Schnabel models we have 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. Or alternatively some animals move around more and are exposed to more traps. This individual variation in chances of capture is called *heterogeneity* in Program CAPTURE, 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 the second, third, fourth..... captures. This source of variation is also common and is labeled *behavior* in Program CAPTURE because it arises in general as a behavioral response of animals to the trapping devices.

These sources of variation can be combined so it is possible to have 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_{TBH} - the full model with time, heterogeneity, and behavior varying

The more complicated models as you might guess are harder to fit to observed data.

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 try to develop better methods of model selection. Program MARK has a model-selection routine that operates for the comparison of some models that use maximum likelihood methods.

The details of the models and the calculations are presented in Otis *et al.* (1978) and for ecologists a general description of the procedures used and some sample data runs are given in Amstrup *et al.* (2006). Maximum-likelihood methods (see Chapter 3 for an example) are used in many of the estimation procedures in CAPTURE, 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:

$$L(\hat{N}_0, \hat{p} | X) = \ln \left(\frac{N!}{(N-M)!} \right) + (n) \ln(n) + (tN - n) \ln(tN - n) - (tN) \ln(tN) \quad (2.17)$$

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 \mathbf{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 \hat{N}_0 .

Once the value of \hat{N}_0 has been determined, the probability of capture can be obtained from:

$$\hat{p} = \frac{n}{t \hat{N}_0} \quad (2.18)$$

where all terms are as defined above. The variance of the estimated population size is obtained from:

$$\hat{Var}(\hat{N}_0) = \frac{\hat{N}_0}{(1-\hat{p})^{-t} - (t/1-\hat{p}) + t - 1} \quad (2.19)$$

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:

$$\hat{N}_0 \pm z_\alpha \sqrt{\hat{Var}(\hat{N}_0)} \quad (2.20)$$

where z_α = 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 tendency for confidence intervals of population estimates to be narrower than they ought to be (Otis *et al.* 1978, p. 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 (2.17) simplifies to:

$$\hat{N}_0 = \frac{(n_1 + n_2)^2}{4m} \quad (3.24)$$

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

For example, from the data in Box 2.1 (page 000) 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 of 2383 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 2.3 gives a sample set of calculations for the null model from Program CAPTURE.

Box 2.3 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 will 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 will 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:

$$\begin{aligned} L(\hat{N}_0, \hat{p} | X) &= \ln \left(\frac{112!}{(112-65)!} \right) + (86) \ln(86) + (5[112]-86) \ln(5[112]-86) \\ &\quad - (5(112)) \ln(5(112)) \\ &= 42.789 \end{aligned}$$

By repeating this calculation for other provisional estimates of N you can determine:

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

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

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

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)

$$\begin{aligned} \hat{Var}(\hat{N}_0) &= \frac{\hat{N}_0}{(1-\hat{p})^{-t} - (t/(1-\hat{p})) + t - 1} \\ &= \frac{121}{(1-0.142)^{-5} - \left(\frac{5}{(1-0.142)} \right) + 5 - 1} = 373.5 \end{aligned}$$

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

$$\begin{aligned} \hat{N}_0 \pm z_{\alpha} \sqrt{\hat{Var}(\hat{N}_0)} \\ 121 \pm 1.645 \sqrt{373.5} \text{ or } 121 \pm 32 \end{aligned}$$

These calculations including confidence limits can be done by Program CAPTURE or Program MARK and these methods are discussed in detail by Cooch and White (2010).

Program MARK is a very complex model for mark-recapture analysis and if you are involved in mark-recapture research it will repay the large investment you need to

put into learning how to use it. It is currently the gold standard for mark-recapture analysis. Program CAPTURE is much simpler to understand but cannot do the elegant analyses implemented in Program MARK. Box 2.4 illustrates a data set for snowshoe hares and the resulting CAPTURE estimates.

Box 2.4 Use of Program CAPTURE to Estimate Population Size for Snowshoe Hares

Krebs et al. (2001) obtained these data from live trapping of snowshoe hares on a 25 ha grid in the Yukon in 2004. The data are summarized in an **X-matrix** format. The first number is the ear tag number of the individual, and the 1 and 0 indicate whether or not it was captured in session 1, 2, 3, or 4. For example, hare 2045 was captured only in session 4.

```

2153 1111
2154 1101
2155 1100
2035 1101
2039 1101
2040 1001
2041 1000
2207 1111
2205 1110
2208 1100
2084 1101
2210 1101
2211 1001
2083 1100
2218 0111
2042 0111
2043 0101
2045 0001

```

The first estimates CAPTURE provides is of the probable model which has the best fit to the data. For these data the program gives:

Model selection criteria. Model selected has maximum value.

Model	M(o)	M(h)	M(b)	M(bh)	M(t)	M(th)	M(tb)	M(tbh)
Criteria	0.14	0.00	0.09	0.15	0.91	1.00	0.45	0.34

The best model appears to be M_{TH} , followed closely by M_T

To illustrate Program CAPTURE estimates we calculated population estimates for all the models available using the format for data in CAPTURE. The results of the computer run were the following estimates of \hat{N} for these 18 hares:

M_0 - the null model: 18 (95% likelihood interval 18-19)

M_T - the time model (Chao) : 18 (18-20)

M_H - the heterogeneity model (Jackknife): 20 (19-26)

M_B - the behavior model (Zippin): 18 (18-19)

M_{TH} - the time and heterogeneity model: 21 (19-31)

M_{TB} - the time and behavior model: 18 (18-20)

M_{BH} - the behavior and heterogeneity model (Generalized Removal): 18 (18-19)

M_{TBH} - the full model with time, heterogeneity, and behavior varying: 21 (19-36)

In this case all of the estimates are very close to one another. This is partly because the probability of capture of an individual hare averaged over all the four trapping sessions is estimated to be about 64%. Estimates of populations are much more precise when the probability of capture is high. Estimates are further improved by having more trapping sessions.

There is a great deal of sophisticated mathematics buried in these programs and you should be aware of the assumptions you make to use these methods.

These calculations including confidence limits can be done by Program CAPTURE or Program MARK and these methods are discussed in detail by Otis *et al.* (1978) and Cooch and White (2010).

We will discuss alternative approaches to closed population estimation in Chapter 3.

2.4 CORMACK-JOLLY-SEBER METHOD

Both the Petersen and Schnabel methods as well as the closed population models implemented in Programs CAPTURE and MARK are designed for populations that are not changing in size during the sampling period. We now extend the mark-recapture technique to the more biologically realistic situation of *open* populations. The open population model now used was developed jointly by Richard Cormack, George Jolly, and George Seber, and is now commonly referred to as the Cormack-Jolly-Seber model (or CJS for short).

Most populations are constantly changing in size because of births, deaths, immigration, and emigration. The procedure for obtaining estimates from an open population is as follows. Mark-recapture samples are taken on three or more occasions. Individuals are marked with numbered tags or any mark which is specific to the sampling time. The important point here is to be able to answer for each marked animal in the sample: *When was this marked individual last captured?* Often animals are

tagged individually so that data on movements can also be collected at the same time as population estimation is done. The samples are usually point samples of short duration, and separated by a long duration from the next sample. The time interval between samples need not be constant, and any number of samples can be accommodated so that series of data extending over many years can be used in this method.

Before we discuss the estimation procedures, let us get a good grasp of the data used in the calculations. All the animals in the first sample must be unmarked by definition. For the second and all subsequent samples the total catch can be subdivided into two fractions - *marked animals* and *unmarked animals*. For marked individuals we ask one important question: when was this individual *last* captured? Leslie (1952) showed that this was the most informative question to ask about marked individuals, better for example than asking when it was first captured. The answers to this question are tallied in a Method B table (Leslie and Chitty 1951). Table 2.3 gives a Method B table for a series of 11 samples from a field vole population.

It will help you to understand the contents of a Method B table to go through some of the details given in Table 2.3. In the second sample all of the 15 marked voles must have been last caught in the first sample. But in the third sample marked animals may have been last caught at time 2 (15) or time 1 (1). Marked individuals may thus evade capture for one or more sampling periods. In an intensive mark-release program, most of the marked animals caught will have been last caught at the previous sampling, and consequently will appear along the subdiagonal of the method B table. Conversely, when populations are very large or sampling less intensive, more and more recaptures will appear above the subdiagonal of the method B table, since marked individuals will typically evade capture for several sampling periods in this situation.

TABLE 2.3 Mark recapture data for a series of 11 samples a field vole (*Microtus pennsylvanicus*) population in the southwestern Yukon^a. Three rectangles are outlined in the table to illustrate the captures counted for three of the variables in the calculations. See the text for an explanation.

Time of last capture	Time of Capture										
	1	2	3	4	5	6	7	8	9	10	11
1		15	1	0	0	0	0	0	0	0	0
2			15	0	1	0	0	0	0	0	0
3				37	2	0	0	0	0	0	0
4					61	4	1	1	0	0	0
5						75	3	2	0	0	0
6					$m_6 \nearrow$		77	4	0	0	0
7						$R_6 \nearrow$		69	0	0	0
8									8	1	0
9										14	0
10											19
Total marked (m_t)	0	15	16	37	64	79	81	76	8	15	19
Total unmarked (u_t)	22	26	32	45	25	22	26	15	11	12	3
Total caught (n_t)	22	41	48	82	89	101	107	91	19	27	22
Total released (s_t)	21	41	46	82	88	99	106	90	19	26	22

^a Each sample was captured over 2 days, and samples were usually 2 weeks apart. The data are cast in a Method B table as a preliminary to the estimation of population size by the Cormack-Jolly-Seber method.

Given a method B table, we can now define the following variables using the terminology of Jolly (1965):

m_t = number of marked animals caught in sample t

u_t = number of unmarked animals caught in sample t

n_t = total number of animals caught in sample t

$$= m_t + u_t$$

s_t = total number of animals released after sample t

$$= (n_t - \text{accidental deaths or removals})$$

m_{rt} = number of marked animals caught in sample t last caught in sample r

All these variables are symbols for the data written in the method B table. For example, Table 2.3 shows that

$$m_6 = 75 + 4 + 0 + 0 + 0 = 79 \text{ voles}$$

We require two more variables for our calculations,

R_t = number of the s_t individuals released at sample t and caught again in some later sample

Z_t = number of individuals marked *before* sample t , not caught in sample t , but caught in some sample after sample t

These last two variables are more easily visualized than described (see the rectangles in Table 2.3). For example, as shown in the table,

$$R_6 =$$

$$77 + 4 + 0 + 0 + 0 = 81 \text{ voles}$$

The Z_t are those animals that missed getting caught in sample t , and survived to turn up later on. In an intensive mark-release program, the Z_t values will approach zero. In this table for example

$$Z_6 = 3 + 2 + 1 + 1 = 7 \text{ individuals}$$

We can now proceed to estimate population size following Jolly (1965) from the simple relationship:

$$\text{Population size} = \frac{\text{Size of marked population}}{\text{Proportion of animals marked}}$$

The proportion of animals marked is estimated as:

$$\hat{\alpha}_t = \frac{m_t + 1}{n_t + 1} \quad (2.17)$$

where the "+ 1" is a correction for bias in small samples (Seber 1982, p. 204). The size of the marked population is more difficult to estimate because there are two components of the marked population at any sampling time: (1) marked animals actually caught; and (2) marked animals present but not captured in sample t . Seber (1982) showed that the sizes of the marked population could be estimated by:

$$\hat{M}_t = \frac{(s_t + 1)Z_t}{R_t + 1} + m_t \quad (2.18)$$

where M_t = estimated size of the marked population just before sample time t

We can now estimate population size:

$$\hat{N}_t = \frac{\hat{M}_t}{\hat{\alpha}_t} \quad (2.19)$$

where \hat{N}_t = estimated population size just before sample time t

Table 2.4 gives these estimates for the data in Table 2.3, and a few sample calculations follow:

$$\hat{\alpha}_5 = \frac{64+1}{89+1} = 0.7222$$

$$\hat{\alpha}_6 = \frac{79+1}{101+1} = 0.7843$$

$$\hat{M}_2 = \frac{(41+1)(1)}{16+1} + 15 = 17.47$$

$$\hat{M}_6 = \frac{(99+1)(7)}{81+1} + 79 = 87.54$$

$$\hat{N}_2 = \frac{87.54}{0.7843} = 111.6$$

We can derive an additional bonus from the use of the Cormack-Jolly-Seber Model of population estimation - an estimate of the loss rate and the addition rate of the population. Consider first the loss rate. We define

Φ_t = probability of surviving from sample time t to sample time $t + 1$

$$= \frac{\text{Size of marked population at start of sample time } t + 1}{\text{Size of marked population at end of sample time } t}$$

The marked population is added to during each sampling time as new individuals are marked and released. Thus the size of the marked population at the end of sample t consists of the marked individuals alive at the start of t plus the new individuals marked during sampling time t , or in the symbols defined above:

$$\hat{\Phi}_t = \frac{\hat{M}_{t+1}}{\hat{M}_t + (s_t - m_t)} \quad (2.20)$$

This formula corrects for all accidental deaths or removals at time t . Note that the probability of surviving is determined by sampling the *marked population* only. Survival in this context means staying alive on the study area. Individuals which emigrate are counted as losses in the same way as individuals that die.

An addition rate to the population is called the *dilution rate*^{*}, since it includes both additions by births and by immigration:

$$\begin{aligned}\lambda_t &= \text{dilution rate from sample time } t \text{ to sample time } t+1 \\ &= \frac{\text{Actual population size at sample time } t+1}{\text{Expected populations size at sample time } t+1 \text{ if no additions occurred}}\end{aligned}$$

The expected population size in the absence of any gains is clearly:

$$\left\{ \begin{array}{l} \text{Expected population} \\ \text{size at time } t+1 \end{array} \right\} = \left(\begin{array}{l} \text{Probability of survival} \\ \text{from } t \text{ to } t+1 \end{array} \right) \left(\begin{array}{l} \text{Population size} \\ \text{at time } t \end{array} \right)$$

and once we correct for accidental deaths we obtain:

$$\hat{\lambda}_t = \frac{\hat{N}_{t+1}}{\hat{\Phi}_t [\hat{N}_t - (n_t - s_t)]} \quad (2.21)$$

Thus if there are no additions at all, we expect the dilution rate to be 1.0, its theoretical minimum value.

From a series of population estimates we can define:

$$\text{Finite rate of population change} = \frac{N_{t+1}}{N_t}$$

if there are no accidental deaths at time t . By rearranging formula (2.21) we see for the ideal case of no accidental losses ($n_t = s_t$):

$$\Phi_t \lambda_t = \frac{N_{t+1}}{N_t} = \text{Finite rate of population change} \quad (2.22)$$

* Note that the *dilution rate* defined here follows Jolly (1965) and differs from that of Leslie *et al.* (1953) who defined a dilution factor that is zero when there is no dilution.

Thus when there are no losses ($\Phi_t = 1.0$) and no additions ($\lambda_t = 1.0$) the population remains constant.

The addition rate to the population can also be expressed as a *number* of individuals: If we define

$$B_t = \left\{ \begin{array}{l} \text{Number of new animals joining the population between} \\ \text{time } t \text{ and } t+1 \text{ and still alive at time } t+1 \end{array} \right\} \quad (2.23)$$

$$\hat{B}_t = \hat{N}_{t+1} - \hat{\Phi}_t [\hat{N}_t - (n_t - s_t)]$$

and this formula is clearly just a rearrangement of formula (2.21).

It is important to keep in mind that these estimates of N_t , Φ_t , λ_t , and B_t are *not* independent estimates of what is happening in a population, but they are all interconnected so that when one estimate is poor they are all poor.

Estimates of population size (N_1) and dilution rate (λ_1) cannot be obtained for the first sample, nor can any of these parameters be estimated for the last sample (see Table 2.4). In addition the probability of survival cannot be estimated for the next to last sample (Φ_{s-1}). For this reason population studies using the Cormack-Jolly-Seber model should be planned to start before the time periods of interest and extend at least two samples beyond the last time periods of interest.

2.4.1 Confidence Intervals for Cormack-Jolly-Seber Estimates

Variances for the estimates of population size, probability of loss, and dilution rate are given in Jolly (1965) but these are valid only for large size samples. Manly (1971) and Roff (1973) have shown with computer simulation that the large-sample variances are not reliable for getting confidence intervals because the estimated confidence belt is too narrow. Manly (1984) suggested an alternative method of obtaining confidence limits for Cormack-Jolly-Seber estimates. Manly's methods of obtaining confidence limits for the Cormack-Jolly-Seber model have been criticized as being slightly arbitrary by Pollock *et al.* (1990) but since they work reasonably well, we will present them here.

Confidence limits for population size Transform the estimates of N_t by:

$$T_1(\hat{N}_t) = \log_e(\hat{N}_t) + \log_e \left[\frac{1 - (p_t/2) + \sqrt{1 - p_t}}{2} \right] \quad (2.24)$$

where $\hat{p}_t = \frac{n_t}{\hat{N}_t} = \frac{\text{Total caught at time } t}{\text{Estimated population size at time } t}$

The variance of this transformation is given by:

$$\hat{\text{Var}}[T_1(\hat{N}_t)] = \left(\frac{\hat{M}_t - m_t + s_t + 1}{\hat{M}_t + 1} \right) \left(\frac{1}{R_t + 1} - \frac{1}{s_t + 1} \right) + \frac{1}{m_t + 1} - \frac{1}{n_t + 1} \quad (2.25)$$

The upper and lower 95% confidence limits for T_1 are given by:

$$T_{1L} = T_1(\hat{N}_t) - 1.6\sqrt{\hat{\text{Var}}[T_1(\hat{N}_t)]} \quad (2.26)$$

$$T_{1U} = T_1(\hat{N}_t) + 2.4\sqrt{\hat{\text{Var}}[T_1(\hat{N}_t)]} \quad (2.27)$$

where T_{1L} = lower confidence limit for T_1
 T_{1U} = upper confidence limit for T_1

The confidence limits for population size are then:

$$\frac{(4L + n_t)^2}{16L} < \hat{N}_t < \frac{(4U + n_t)^2}{16U} \quad (2.28)$$

Table 2.4 Population estimates derived from data in Table 2.3 by use of the Cormack Jolly-Seber model of population estimation for an open population. Eleven samples from a field vole population in the southwestern Yukon.

Sample	Proportion marked	Size of marked population	Population estimate N_t	Probability of survival ϕ_t	Number joining B_t	Standard errors of		
						N_t	ϕ_t	B_t
1	.000	0.0	— ^a	.832	—	—	.126	—
2	.381	17.5	45.9	.395	31.4	6.1	.077	2.7
3	.347	17.2	49.5	.862	47.9	4.0	.055	3.6
4	.458	40.7	88.8	.824	24.6	5.3	.043	3.3
5	.722	70.5	97.7	.925	22.1	5.3	.032	2.6
6	.784	87.5	111.6	.853	27.3	5.8	.043	2.8
7	.759	91.7	120.8	.651	12.8	7.1	.046	1.7
8	.837	76.0	90.8	.104	11.4	6.5	.033	1.8
9	.450	9.3	20.7	.738	10.9	3.6	.101	1.1
10	.571	15.0	26.2	—	—	4.4	—	—
11	.870	—	—	—	—	—	—	—

^a — means that no estimate can be made of this parameter from the data available.

where $L = e^{T_{1L}}$
 $U = e^{T_{1U}}$
 $e = 2.71828....$ (the base of natural logarithms)

where $L = e^{T_{1L}}$
 $U = e^{T_{1U}}$
 $e = 2.71828....$ (the base of natural logarithms)

These confidence limits will not be symmetrical about \hat{N}_t .

Confidence limits for probability of survival Transform the estimates of Φ_t as follows:

$$T_2(\hat{\Phi}_t) = \log_e \left(\frac{1 - \sqrt{1 - A_t \Phi_t}}{1 + \sqrt{1 + A_t \Phi_t}} \right) \quad (2.29)$$

where $A_t = \frac{C_t}{B_t + C_t}$

(B_t and C_t are defined below). The variance of this transformed value of Φ_t is:

$$\hat{Var}[T_2(\Phi_t)] = B_t + C_t \quad (2.30)$$

where

$$\begin{aligned} \hat{B}_t &= \left[\frac{(\hat{M}_{t+1} - m_{t+1} + 1)(\hat{M}_{t+1} - m_{t+1} + s_{t+1} + 1)}{(\hat{M}_{t+1} + 1)^2} \right] \\ &\quad \times \left(\frac{1}{R_{t+1} + 1} - \frac{1}{s_{t+1} + 1} \right) + \left(\frac{\hat{M}_t - m_t + 1}{\hat{M}_t - m_t + s_t + 1} \right) \\ &\quad \times \left[\left(\frac{1}{R_t + 1} - \frac{1}{s_t + 1} \right) \right] \\ \hat{C}_t &= \frac{1}{\hat{M}_{t+1} + 1} \end{aligned}$$

The upper and lower 95% confidence limits for T_2 are given by:

$$\hat{T}_{2L} = T_2(\hat{\Phi}_t) - 1.9\sqrt{\hat{\text{Var}}[T(\hat{\Phi}_t)]} \quad (2.31)$$

$$\hat{T}_{2U} = T_2(\hat{\Phi}_t) + 2.1\sqrt{\hat{\text{Var}}[T(\hat{\Phi}_t)]} \quad (2.32)$$

The confidence limits for the probability of survival are then:

$$\frac{1}{A_t} \left[1 - \frac{(1-L)^2}{(1+L)^2} \right] < \hat{\Phi}_t < \frac{1}{A_t} \left[1 - \frac{(1-U)^2}{(1+U)^2} \right] \quad (2.33)$$

where

$$L = e^{T_{2L}}$$

$$U = e^{T_{2U}}$$

$$A_t = \frac{C_t}{B_t + C_t} \text{ as defined above.}$$

There are at present no simple estimates for the confidence limits of the dilution rate.

These formulae can be calculated by a computer program. Program RECAP in Appendix 2 (page 000) computes the Cormack-Jolly-Seber estimators of population size, probability of survival, and dilution rate, along with the confidence limits from Manly (1984). Program MARK and Program DENSITY 4 (see Chapter 3) calculate these estimates as well.

The Cormack-Jolly-Seber model can be considerably simplified if some of the parameters of the model are constant. Jolly (1982) discusses four versions of the Cormack-Jolly-Seber model:

- (1) **Model A** - the full Cormack-Jolly-Seber model as discussed above in which all parameters may change from sampling period to sampling period.
- (2) **Model B** - the constant survival model, which assumes that loss rates are constant over the entire period of sampling, so that only one loss estimate must be calculated.
- (3) **Model C** - the constant capture model, which assumes that the probability of capture remains constant for all animals over all the entire sampling periods.
- (4) **Model D** - the constant survival and constant capture model which assumes both constant survival and constant capture probabilities during the study period. This is the simplest model.

If any of these reduced models B, C, or D is appropriate for your data, you can gain considerably in precision by adopting the reduced model. All these models involve maximum likelihood estimation so that they can be solved only with the help of a computer. Pollock *et al.* (1990) describe Program JOLLY which will carry out these calculations and Program MARK will also do these calculations for reduced models.

2.4.2 Assumptions of the Cormack-Jolly-Seber Method

The Cormack-Jolly-Seber method is designed for open populations, so unlike the earlier methods discussed in this chapter we do not need to assume the absence of recruitment and mortality. Random sampling becomes the crucial assumption, and we assume:

1. Every individual has the same probability (α_t) of being caught in the t -th sample, regardless whether it is marked or unmarked
2. Every marked individual has the same probability (Φ_t) of surviving from the t -th to the $(t+1)$ -th sample
3. Individuals do not lose their marks and marks are not overlooked at capture
4. Sampling time is negligible in relation to intervals between samples.

The critical assumption of equal catchability for marked and unmarked individuals must be tested before you can rely on estimates provided by the Cormack-Jolly-Seber model or indeed by any mark-recapture model.

2.5 PLANNING A MARK-RECAPTURE STUDY

The most important message this chapter should give you is that you must plan a mark-recapture study carefully in advance to avoid being disappointed by the precision of your results. Pollock et al. (1990) have provided an excellent discussion of how to plan marking experiments, and I summarize here some of their important suggestions.

The equal catchability assumption is the Achilles heel of all estimation that utilizes marking animals. In some cases you can adjust your study to minimize violations in this assumption. For example, if juvenile animals have a much lower chance of capture, you can separate adults and juveniles in your data. If a shortage of traps limits catchability, you might increase the number of traps available. One design that is useful to consider is the robust capture-recapture design first suggested by Pollock (1982). The robust design involves the use of two methods of estimation, an open method like the Cormack-Jolly-Seber model and a closed method like the Schnabel method or the CAPTURE models described above. Figure 2.7 illustrates the robust design.

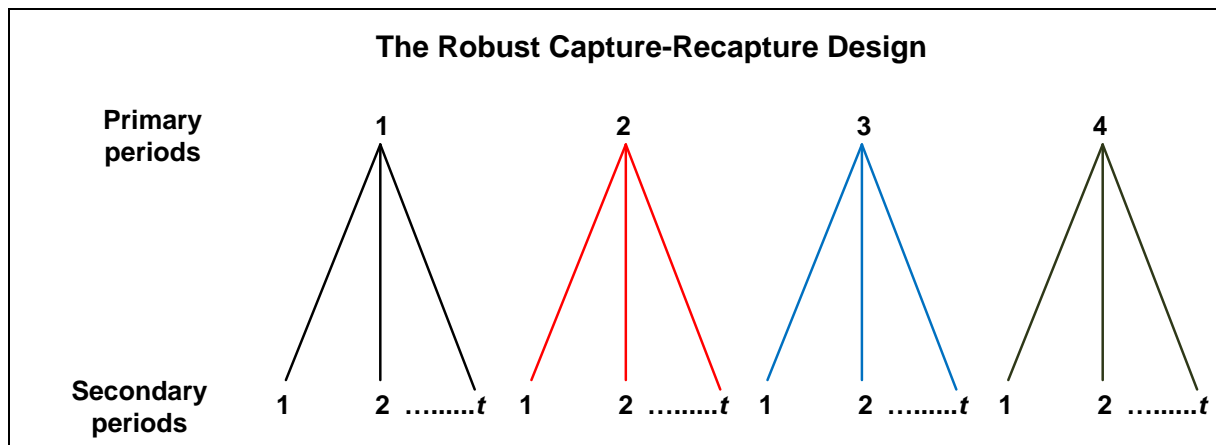


Figure 2.7 Schematic representation of the robust design of Pollock (1982) for mark-recapture studies. A primary period might be one week, and within the week secondary periods might be the animals captured each day. Closed population estimators can be used for the secondary periods, and open estimators like the Cormack-Jolly-Seber model can be used for the capture data grouped into the primary periods.

Primary sample periods might be weeks or months, and within these periods are secondary periods of capture of short duration (e.g. days or hours). For example, for rodents primary periods might be months and secondary periods a series of 6 daily samples. For large birds, primary periods might be years and secondary periods a series of 5 weekly samples. The data for the Cormack-Jolly-Seber calculations are obtained by pooling the data from the secondary periods. Recaptures within the secondary periods make no difference for the Cormack-Jolly-Seber calculations but are essential information for closed population estimators like the CAPTURE models.

The strength of the robust design is in the fact that survival rates estimated by the Cormack-Jolly-Seber model are insensitive to variations in catchability, and population estimates from some closed models like CAPTURE can take unequal catchability into account to get a relatively unbiased estimate of population size. Given these two parameters, we can use equation (2.23) to estimate the number of births in the population. Population estimates derived from the Cormack-Jolly-Seber model are very sensitive to deviations from equal catchability, and the robust design avoids relying on this model for an unbiased estimate of population size.

To use the robust design it is useful to determine what level of sampling intensity is needed to provide reliable estimates. As a measure of precision, we will use the coefficient of variation. For population estimates, this is:

$$CV(\hat{N}) = \frac{\sqrt{\text{Var}(\hat{N})}}{\hat{N}} \quad (2.34)$$

The smaller the coefficient of variation, the higher the precision. A rough rule of thumb is that a CV of 0.20 (or 20%) is reasonable for ecological work. Pollock *et al.* (1990) have provided a series of figures to assist ecologists in planning how to sample to achieve a CV of 20%. Figure 2.9 illustrates one of these figures for a range of population sizes from 50 to 500 and a range of survival rates from low to high.

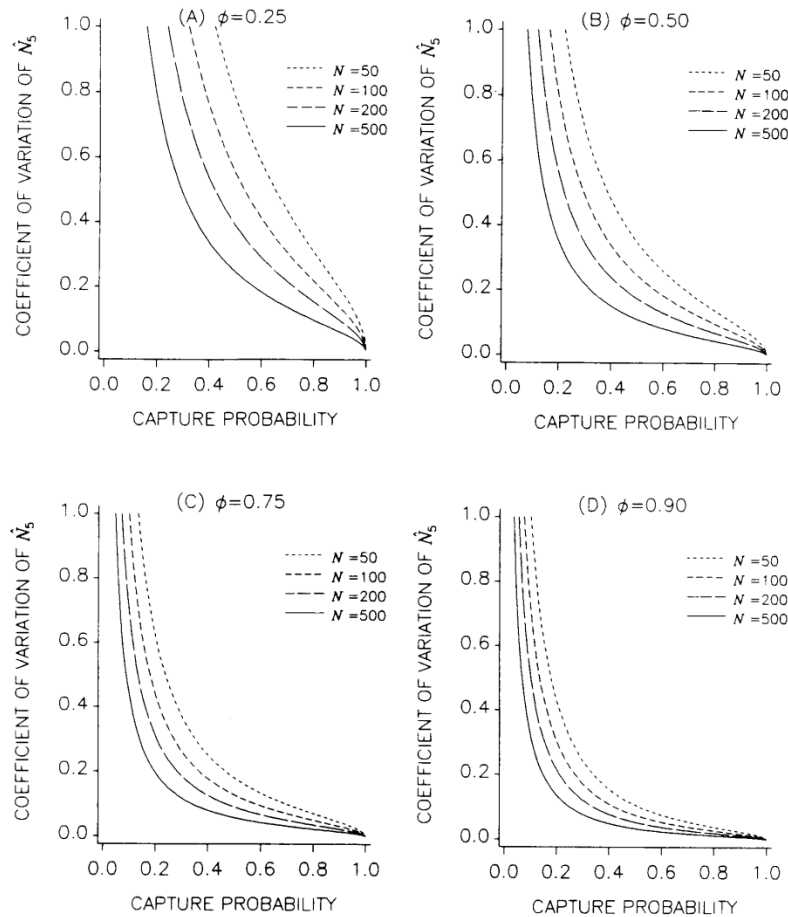


Figure 2.8 Relative precision of the Cormack-Jolly-Seber estimate of population size for a range of population sizes from 50 to 500 when there are 10 sampling periods and the survival rate ϕ varies from 0.25 to 0.90 per primary interval. (From Pollock *et al.* (1990).

Four general principles are illustrated in this graph:

1. Precision increases as the capture probability of individuals increases.
2. As the number of sampling times increases, precision increases.

3. If survival rates are higher, precision is also higher.

4. Precision increases as population size increases, for fixed survival rates, number of samples, and capture probability.

For Cormack-Jolly-Seber estimates, the precision of estimating survival probabilities is nearly the same as that of estimating population size, but it is more difficult to estimate birth rates. Figure 2.9 illustrates this difference for one set of population parameters. Capture probabilities must typically be above 0.80 to achieve high precision in estimates of the birth rate (λ_t or B_t) for populations of 200 or less.

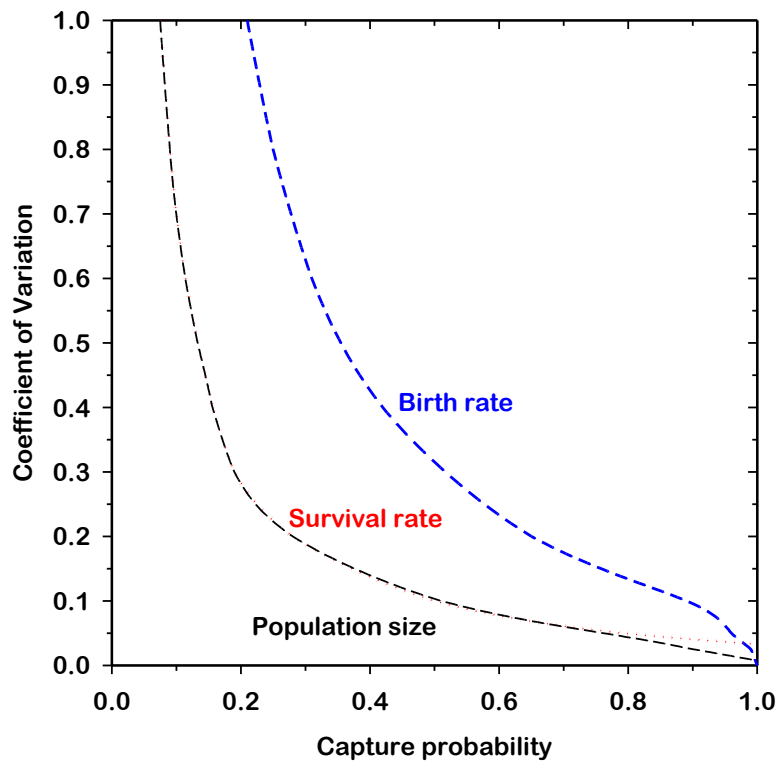


Figure 2.9 Relative precision of Jolly-Seber estimates of population size, survival rate, and birth rate for a hypothetical population of 200 individuals, 10 sample periods, and a survival rate of 0.75. The population size (black) and survival rate (red) curves are nearly identical. The birth rate (blue) is more difficult to estimate with high precision. (From Pollock *et al.* 1990.)

2.6 WHAT TO DO IF NOTHING WORKS

Estimating population size by mark-recapture may be your goal, but may also be unachievable. The assumptions you must make to use any method of estimation may be violated, and the question is what to do in these cases. Four general strategies can be used. First, you can examine more closely the assumptions as they apply to your particular population and try to design new ways of satisfying them. Perhaps random sampling is needed rather than systematic sampling (Chapter 8, page 000). Perhaps a second type of sampling gear can be used to catch some of the samples. Perhaps the

interval between sampling should be longer or shorter. Perhaps the two sexes should be separated in the analysis, or even sampled with different kinds of traps. I call this the *tinkering strategy* since the aim is to alter your techniques to satisfy the existing methods. Program MARK is very good at implementing some of these methods (e.g. testing for differences between the sexes).

A second strategy is to use a very general, empirical model of population estimation. Caughley (1977, p. 152) has reviewed this approach and emphasized its value for practical work. The major assumption of these general models is that the population is closed so there is no mortality during the marking experiment, and consequently they are useful only for intensive short-term sampling. The basic data of these models are the number of individuals caught once, twice, three times and so on (frequency of capture approach). These data form a zero-truncated frequency distribution of captures, and the missing zero- class represents the unknown number of individuals that were never caught. A variety of statistical distributions can be fitted to these data, and one stops once a "good fit" is achieved. Figure 2.10 illustrates this approach and Caughley (1977) provides details for the necessary calculations, included in a Fortran computer program available in Program RECAP (Appendix 2, page 000).

Chao (1988) provided another approach to data on frequency of capture data. She used data from known populations enclosed in a fence to test the accuracy of her approach. She presented two estimators, depending on whether the majority of animals were caught 1-2 times or 1-3 times. The simplest Chao estimator is given by:

$$\hat{N} = S + \left[f_1^2 / (2f_2) \right] \quad (2.35)$$

where S is the number of individuals caught in the t samples

f_1 is the number of animals caught only once

f_2 is the number of animals caught twice

If there are sufficient numbers of individuals caught 3 times, the modified Chao estimator is given by:

$$\tilde{N} = S + \left[f_1^2 / (2f_2) \right] \left[1 - \{2f_2\} / (tf_1) \right] / \left\{ \left[1 - (3f_3) \right] / (tf_2) \right\} \quad (2.36)$$

which uses the numbers of animals caught once, twice, and three times in the t samples. These estimators can be calculated in Program CAUGHLEY (Appendix 2).

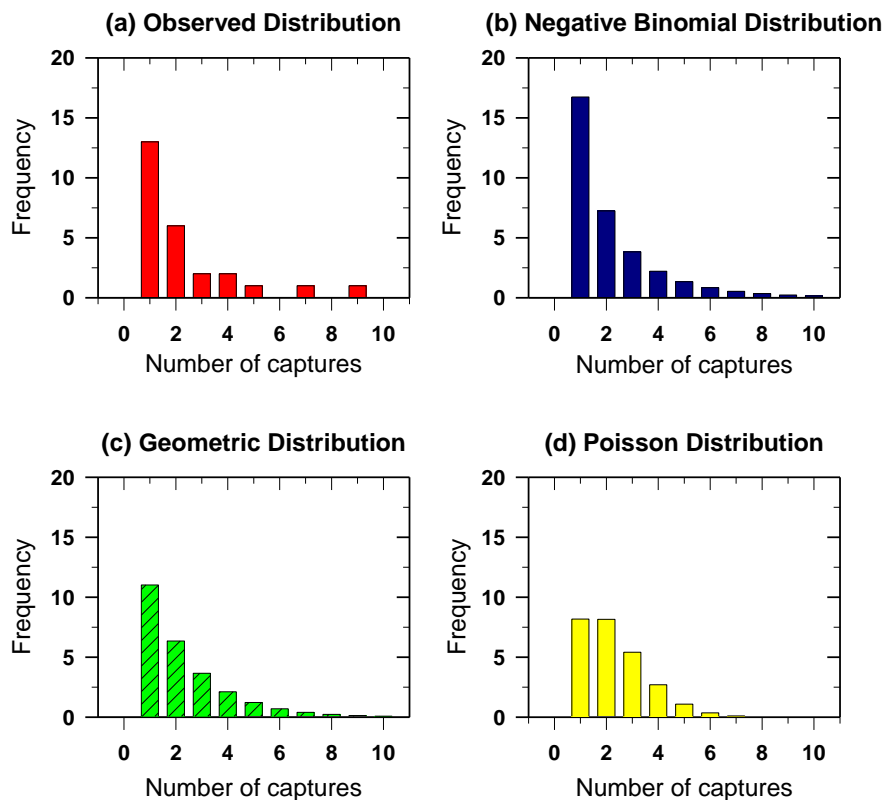


Figure 2.10 Frequency of capture models of population estimation. An observed distribution of frequency of captures (a) is used as a template and several theoretical statistical distributions are fitted - (b), (c), and (d). The theoretical distribution with the closest fit is used to extrapolate to the zero class, those animals that missed getting caught. In this case the geometric distributions fits best because it has the smallest deviation of (observed - expected) values, and a population estimate of 45 is obtained with 19 animals in the zero class ("unseen"). Data on 26 male agamid lizards from Caughley (1977, p. 153).

A third strategy is to change the approach you originally had and to use other methods of estimation included in Chapters 3, 4, and 5. Mark-recapture methods may not be useful for many populations and other forms of census may be more reliable. Perhaps quadrat sampling can be employed or line transect methods. Some populations can be counted *in toto* if enough effort can be employed.

The fourth and final strategy is to use the mark-recapture methods and recognize that the resulting estimates are biased (Jolly and Dickson 1983). Biased estimates may be better than no estimates, but you should be careful to use these estimates only as *indices* of population size. If the bias is such as to be consistent over time, your biased estimates may be reliable indicators of changes in a population.

The principal recommendations of this chapter can be summarized as three rules of procedure:

- **Rule 1:** Evaluate your objectives *before* starting, and do *not* assume that mark-recapture methods are the easiest path to valid population estimates.
- **Rule 2:** Pick your mark-recapture method *before* starting field work, and build into your sampling program a test of the model's assumptions.
- **Rule 3:** Treat all population estimates and confidence intervals with caution, and recheck your assumptions as often as possible.

There is a considerable literature on more specialized techniques of mark-recapture estimation. Seber (1982), Amstrup et al. (2006) and Cooch and White (2010) cover all these problems in more detail.

2.7 SUMMARY

In both population and community ecology the single most important variable that must be estimated is the size of a particular population or series of populations. One way to do this is to use *mark-recapture* methods. Two general types are available, depending on whether the population is *closed* or *open*.

Closed populations do not change in size during the sampling period, and thus sampling must be done over a short time period. When only one period of marking and recapture is available, the *Petersen* method is appropriate. When several samples are taken with marking and recapturing, the *Schnabel* method or the *Schumacher-Eschmeyer* method can be used. More advanced models are available in Program CAPTURE and Program MARK if individuals are tagged and 3 or more sampling sessions are carried out. The assumptions that are most critical are that sampling is random and that marking animals does not affect their catchability. A test of these assumptions is critical in any mark-recapture study.

Open populations change in size continuously, and the *Cormack-Jolly-Seber* model is the best for analysis. The critical question for each marked individual caught is: *when was this individual last caught?* Populations can be sampled over many years with this approach, and in addition to population estimates, the Cormack-Jolly-Seber model provides estimates of the probability of survival and the recruitment (dilution) rate between the sampling times. For long term studies a *robust design* is recommended in which both open and closed estimators can be applied to the recapture data.

One critical assumption of all mark-recapture models is that animals are equally catchable, so that marked individuals at any given sampling time have the same chances of capture as unmarked individuals. This assumption is often violated in natural populations, and statistical models in CAPTURE and MARK can test this critical assumption in a variety of sampling situations with closed populations.

Mark-recapture techniques are difficult to use in the real world, and you should be certain they are needed before starting to use these techniques. A guide to the intensity

of sampling required to attain reliable data is provided for open populations. High capture probabilities are typically needed to obtain reliable data. For many organisms there are easier ways of estimating abundance. The next three chapters describe some alternative approaches.

SELECTED READING

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- Pollock, K.H., J.D. Nichols, C. Brownie, and J.E. Hines. 1990. Statistical inference for capture-recapture experiments. *Wildlife Monographs* **107**: 1-97.
- Seber, G.A.F. 1982. *The Estimation of Animal Abundance and Related Parameters*. 2nd edition. Griffin, London.
- White, G.C. 2008. Closed population estimation models and their extensions in program MARK. *Environmental and Ecological Statistics* **15**(1): 89-99.
- Williams, B.K., Nichols, J.D., and Conroy, M.J. 2002. *Analysis and Management of Animal Populations*. Academic Press, New York.

QUESTIONS AND PROBLEMS

2.1. Villette (2010) marked red-backed voles with ear tags and recaptured them the following morning by live trapping. She got these results for August 2009

number marked and released on day 1 = 48

number of caught on day 2 = 57

number caught on day 2 that were already marked = 40

She got these results for July 2010:

number marked and released on day 1 = 9

number of caught on day 2 = 9

number caught on day 2 that were already marked = 7

Calculate population estimates and their 95% confidence limits for these two data sets. What assumptions must you make to calculate this estimate?

- 2.2.** Wood (1963) sampled climbing cutworms at night, marked them with a fluorescent powder, and resampled the population the next night. He obtained these data for 1962:

M = 1000 (first night)

C = 1755 second night

R = 41

Calculate the estimated population size and its 95% confidence interval for these data.

- 2.3.** Hayne (1949) marked and released meadow voles in Michigan over five days with the following results:

Date	Total catch	No. marked	No. accidental deaths
July 19 p.m.	8	0	0
July 20 a.m.	19	0	0
July 20 p.m.	10	2	1
July 21 a.m.	23	8	0
July 21 p.m.	9	0	0
July 22 a.m.	14	9	0
July 22 p.m.	9	7	1
July 23 a.m.	21	13	0

Calculate an appropriate estimate of population size and justify your choice of methods.

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

	Mature animals	Immature animals
Number marked at time 1	32	35

	June									40	5
	July										56
Total marked	0	12	17	23	20	28	57	49	57	44	62
Total caught	107	45	85	69	67	106	125	99	117	98	127
Total released	96	41	82	64	64	104	121	89	92	95	127

2.6. Bustard (1969) reported the following summary of recaptures of marked lizards in eastern Australia over 1963-1965:

No. of times recaptured	No. of lizards
1	238
2	91
3	46
4	33
5	15
6	9
7	9
8	10
9	2
10	4
11	1
12	0
13	1
14	3
15	2
19	2

Use Caughley's method (page 78, Figure 2.10) and Chao's estimators (equations 2.35 and 2.36) to estimate the population size of these lizards. What assumptions must you make to use these tests?

2.7. Rose and Armentrout (1974) marked and recaptured aquatic larvae of the tiger salamander in temporary ponds in Texas. For a rough estimate of 1000 salamanders, estimate from Figure 2.4 the sample size they would need for

detailed research data on this population.

They obtained this sample for one pond:

No. Tagged on days 1-3 = 552

No. Captured on day 4 = 312

No. Tagged Individuals on day 4 = 200

Calculate the population estimate for these data, and compare with the known value of 875 salamanders for this pond. Was the estimated population size close to the true value?

- 2.8.** Carothers (1973) used mark recapture methods to estimate the number of taxi cabs in Edinburgh, Scotland. He could determine that the known population was 420 cabs. In one of his samples over 5 days he obtained these data:

cabs counted only one time = 135

cabs counted twice = 42

cabs counted three times = 9

cabs counted four times = 1

Estimate the size of this population and compare it with the known number of cabs.

- 2.9.** Since all field populations of animals are open populations, why would you ever use closed population estimators to determine population size?

- 2.10.** Is it ever possible to have a Petersen population estimate that is lower than the actual number of individuals caught? Can the lower confidence limits of a Petersen estimate ever be below the actual number of individuals caught?

- 2.11.** Chao (1988) reported capture data on the striped skunk as follows:

Capture frequency	1977 (8 trap nights)	1978 (4 trap nights)
Caught once (f_1)	2	10
Caught twice (f_2)	7	4
Caught three times (f_3)	5	1
Caught four times (f_4)	3	2
Caught five times (f_5)	2	
No. individuals caught	19	17
Known population size	23	28

Calculate the Schnabel and the Chao estimators for these two samples and discuss which estimate is closer to the true value and why.