APPENDIX B
ANSWERS TO QUESTIONS AND EXERCISES

Chapter 1

1. Yes. Each animal can have its own unique probability of capture on each occasion, and this can change after first capture.
2. Yes. Any summary statistic can be computed from the X matrix.
3. Model M_o is not often used in real population work because it makes assumptions that are rarely valid, for example, equal catchability. Moreover, the estimate of N is poor when these assumptions are violated.
4. No. It is extremely important. The biologists must consider fully both demographic and geographic closure before conducting a trapping program. Without geographic closure, N is not even defined and, therefore, $\hat{N}$ is difficult to interpret.
5. a. $t = 7, j = 1, \ldots, t$.
   b. $n_1 = 3$
   $n_2 = 5$
   $n_3 = 3$
   $n_4 = 3$
   $n_5 = 3$
   $n_6 = 3$
   $n_7 = 2$

   These are merely column totals in X:
   $$n_j = \sum_{i=1}^{N} x_{ij} \ .$$
   c. $u_1 = 3 = n_1$ (always).
   $u_2 = 4$.
   d. They are either trap happy (Model M_b) or they are animals that have a high capture probability (Model M_h). You could argue that animal 6 is trap shy, because it was not captured on any of the 5 nights after its first capture.
   e. $M_{t+1} = M_8 = 7$ animals; 7 distinct animals were caught at least once during the study.
   f. $M_1 \equiv 0$; there are no marked animals at the first trapping occasion.
6. No. This situation is not encompassed by Model M_b.
7. No. Under closure, $S \equiv 1$ (no deaths).
8. These sampling methods will provide only an estimate of the parameter N of interest. Tell him to drain the pond and count the fish if he must know the exact population size.
9. The estimators $\hat{p}$ and $\hat{N}$ are closely coupled. The estimates of capture probabilities in the model and the estimate of N are directly related. A good estimate of population size depends on good estimates of capture probabilities. Finally, if p is small, few data will be available for analysis. All the methods perform better if p is large.
10. If you do, you are hallucinating.
11. Very general models usually do not have estimators (for example, Model M_{tbh}), because of the large number of parameters they require. Furthermore, use of a model that is too general will lack the precision that one desires. For example, if you conducted a tutorial ball and urn experiment, the proper model would be M_o. The estimator $\hat{N}$ from this model would have good properties, and the estimated sampling

variance (discussed in detail in Chapter 2) would be small. However, if the ball and urn sample data were analyzed under the more general Model M_h, the estimator $\hat{N}$ would still be unbiased, but the sampling variance would be substantially larger.

12. a. $t = 3$, the number of trapping occasions.
    b. $M_{t+1} = 20$, the number of different animals captured.
    c. $n_1 = 7$, $n_2 = 11$, and $n_3 = 11$, the sum of each column of the X matrix, respectively.
    d. 29 (= 7 + 11 + 11), the total number of captures.
    e. $u_1 = 7$, $u_2 = 9$, $u_3 = 4$.
    f. $f_1 = 13$, $f_2 = 5$, $f_3 = 2$. (Note that $M_{t+1} = f_1 + f_2 + f_3 = u_1 + u_2 + u_3 = 20$.)
    g. $M_1 \equiv 0$, $M_2 = 7$, $M_3 = 16$, and $M_4 = M_{t+1} = 20$.
    h. $M. = 23$.
    i. $m_1 \equiv 0$, $m_2 = 2$, and $m_3 = 7$.
    j. $m. = 9$ ($= m_1 + m_2 + m_3$).

Chapter 2

1. No. See, for example, the equation for $\hat{N}$ from Model M_t in *Otis et al. (1978:106).*
2. Models form the basis from which estimators of parameters can be derived by providing a mathematical expression of the assumptions in terms of parameters. Some parameters such as annual survival rates, cannot be "observed," "measured," or "counted," and models form a basis for estimating them. Estimation procedures developed without an explicit underlying model are termed *ad hoc.*
3. No. It is still just that—an *ad hoc* approach.
4. This is difficult to say, as these answers depend on many factors. As a rough guide, a cv of 10-15% might be useful for research. Management-oriented studies might provide useful results, if the cv were as large as 20-50%, or even larger in some cases.
5. Study 1, unbiased, precise.
   Study 2, biased, precise.
   Study 3, unbiased, not precise.
   Study 4, biased, not precise.
6. T_2 is preferred, because it will reject a false null hypothesis with probability 0.89.
7. Normal, chi-square, F, t, z.
8. H_O: the model fits the data.
   H_A: the model does not fit the data.
9. A true null hypothesis may be rejected (a Type I error) or a false null hypothesis may not be rejected (a Type II error).
10. a. 95% C. I. $= \hat{\theta} \pm 1.96\ \hat{se}(\hat{\theta})$,
    $= 141 \pm 1.96 \times 13.1$,
    $= 115.32$ to 166.68.
    b. It is unlikely that $\theta = 95$ because this value is far outside the interval.
    c. $\theta = 135$ is very plausible: it is close to $\hat{\theta}$ and well within the confidence interval.
11. a. Yes. H_O: $\theta = 95$. H_A: $\theta \neq 95$
    and H_O: $\theta = 135$ H_A: $\theta \neq 135$.
    b. $z = (\theta - \hat{\theta})/\hat{se}(\hat{\theta}) = (141 - 95)/13.1 = 3.51$,
    $z = (\theta - \hat{\theta})/\hat{se}(\hat{\theta}) = (141 - 135)/13.1 = 0.46$.
    c. The test statistic z is distributed normally with a mean of zero and a standard deviation of one. If the significance level of the tests is chosen as 0.05, we can see from Fig. 2.11 that the null hypothesis $\theta = 95$ is rejected, while the null hypothesis $\theta = 135$ is not rejected.

12. Nothing. Without a measure of precision, nothing can be inferred about the true population sizes of the two areas. Tell your colleague to get his act together.

13. a. Lake bass in Wabo tributary of Lake Powell.

b. A census seems impossible—it is better to decide on a sampling method that will provide valid inferences from the sample to the population.

c. Population size of "adult" bass—fish capable of breeding.

d. Capture-recapture or removal sampling should be considered.

e. If N_1 and N_2 are the true population sizes before and after drilling, the hypotheses might be

$$H_0: N_1 = N_2$$
$$H_A: N_1 > N_2.$$

14. No. This is a common misinterpretation of the meaning of a confidence interval. The correct inference is that if the identical study were repeated a large number of times, 95% of such intervals would cover the true parameter.

15. You would conclude that the null hypothesis is false, which is incorrect.

16. a. cv = 0.13, 0.18, 0.22, 0.16, and 0.19, respectively.

b. Yes, cv's of about 20% are reasonable, and each estimate is close to the true parameter value.

c. Probably not. The coefficients of variation are fairly large compared to the actual changes in the population.

17. Until computers became widely available about 10 years ago, approximations had to be made so that the estimation could be done on simple calculating machines.

18. No. However, the more that is known, the better the understanding and interpretation can be.

19. The estimator may be biased, the estimated sampling variance may be too small, or the sample size may be too small. (The normality assumption may not be satisfied.)

20. You can conclude that there is strong evidence that H_0 is false, because if the null hypothesis were true you would expect to observe the data you collected only 7 times in 1000 studies. This is very unlikely, so you reject H_0.

21. $se(\hat{N}) = \sqrt{var(\hat{N})} = \sqrt{625} = 25.$

22. No. We find large biases; the average estimate, computed from the estimator under Model M_t, differs greatly from the parameter N.

Chapter 3

1. No. Equal probability of capture is not necessarily achieved by only a high level of trapping effort. The behavior of the animal also is involved.

2. Yes, often very much so.

3. No, although a removal estimator could be used. Unfortunately, a paper was published claiming that for t = 2, N could be estimated by the Petersen-Lincoln method even when there were no captures (*Bell 1974).*

4. No. It is impossible to get enough captures and recaptures to test assumptions and compute reliable estimates of N_1.

5. Basically, no. If the average capture probability $\bar{p}_1$ for that trapping occasion is known, then $\hat{N} = n_1/\bar{p}_1$, but in practice $\bar{p}_1$ will not be known.

6. No.

7. Model M_t. Yes, if sample sizes are sufficient.

8. All except the number of days of trapping.

9. Model M_o cannot fit these data. Increasing the trapping effort over time will cause average daily capture probabilities to increase, hence to vary with time. Therefore, Model M_t might be the true model, but neither M_h nor M_b can be the true model.

10. (b).
11. No. ML estimates under these models do not exist. One might impose additional assumptions and then obtain an estimator; however, this would change the model. Also, a nonparametric approach might be used to produce an estimator.
12. No. Model M_o is not at all robust. If sample size is small, the power of tests of assumptions is low, and often M_o will appear to fit. This situation (a Type II error) is serious, because M_o is very poor if its assumptions are violated.
13. Because $\hat{N}_h$ (the estimator under Model M_h) is much more robust than $\hat{N}_o$.
14 No. A completely general statistical test for closure is not possible.

Chapter 4

1. Your answer should be an emphatic "No."
2. The most serious defect is that the assumption of constant capture probability cannot be tested, and if that assumption is false the estimator based on it is biased. Even if the constant capture probability model is true, the estimate of N will be very imprecise unless capture probabilities exceed 0.40.
3. No.
4. Yes. Animals are "removed" from the population by marking them.
5. Yes, because there is additional information from recaptures.
6. We certainly hope not.
7. Closure will fail; that is, animals from outside the grid are often attracted by the "vacuum" left by removed animals.
8. If the removal is accomplished by marking, it may be an acceptable plan if the population is large enough, say 750. If removal is by physical detachment, relocations, etc., the proposal is likely to be politically unacceptable. If the removal involves killing the snails, the biologist is in trouble.
9. No. There is clearly no meaningful decline in the numbers removed over occasions 1 to 5. This study has failed.
10. a. Each row of the X matrix has exactly one 1 in it, and the remaining entries are zero. In the first 68 rows, the 1 is in column (occasion) 1. In the next 41 rows, the 1 is in column 2. Then there are 25 rows all with a 1 in column 3, and finally 15 rows with a 1 in column 4. The total matrix is 149 rows by 4 columns.
    b. The study results are acceptable; by looking at the decrease in the removals, we can expect a reasonably precise estimate of N if the constant capture probability model fits.
    c. The simplest "quick and dirty" estimate of N is $M_5 = 149$, which, of course, will be low. The next quick estimate is to use occasions 1 and 2 only and Eq. (4.1),

$$\hat{N} = \frac{u_1}{1 - u_2/u_1} = \frac{68}{1 - 41/68} = 171 \ .$$

    This estimate would suffice to satisfy our curiosity while we still were in the field, but a full-blown analysis requires testing assumptions. We leave it to the reader to apply program CAPTURE to these data.
11. No. The results will be garbage. The expected removals are $E(u_1) = 5$, $E(u_2) = 4.75$, and $E(u_3) = 4.51$.
12. We recommend a capture probability p of at least 0.2, and $p \geq 0.3$ is needed to be sure the results will be reliable.
13. Closure has failed after occasion 3; animals not originally in the population are moving into it.
14. It will be worthless—and very misleading if presented without the evidence from the data that closure has failed.

15. There will be $N - (u_1 + \ldots + u_{j-1})$ individuals left in the population on the j^{th} removal sampling. The average capture probability of these *remaining* individuals is $\bar{p}_j$. If capture probabilities vary in the population, due to innate heterogeneity, then on the first sample individuals with the higher capture probabilities tend to be caught. The individuals remaining (uncaught) on the second removal occasion therefore will have, on the average, lower capture probabilities. Thus, we have $\bar{p}_1 > \bar{p}_2$. By the same argument, the even fewer numbers of individuals remaining after the second removal sample again have smaller average capture probability $\bar{p}_3$, compared to $\bar{p}_2$.
16. Capture probabilities of fish vary greatly by species, and noticeably by fish size, for electrofishing methods. Capture probabilities of small mammals can vary by species, sex, and age; they also can vary due to social dominance and, especially for animals near the edge of the grid, home range size and the number of traps in the home range.
17. Capture probabilities will vary by time, leaving us with an M_{tb} type of model and making estimation of N impossible by removal methods. Catch-effort methods could be used, but then the relative effort on each occasion must be known and quantified and the analysis methods are different from those in *Otis et al. (1978)* or in program CAPTURE (cf. *Seber 1973:296-353*).

Chapter 5

1. No. Nested subgrids could not be constructed, nor would adequate data be obtained.
2. Not necessarily. Animals may not have home ranges that overlap the grid, which implies that $W = 0$, but they may still come and go from the grid, thus violating geographic closure.
3. The number of ellipses that intersect or are contained in the grid.
4. The choice depends on animal density. If all traps are expected to be filled on each occasion, the probability of capture may actually be lowered due to nonavailability of traps. However, all traps usually are not filled, and therefore, one trap per station and a larger grid are preferred. Also, placing the traps at half intervals and using the same size grid is preferable to placing two traps per station.
5. No. Subgrids consisting of halves or quarters are biased when a linear gradient in density exists across the grid. Nested subgrids are robust to such a gradient; that is, they will produce an unbiased estimate of the *average* density in the grid.
6. No. Nested subgrids cannot be constructed from one long line of traps.
7. The additional area included in the strip of width $\hat{W}$ around the grid enlarges the area $\hat{A}$ to which $\hat{N}$ applies, so that $\hat{D} = \hat{N}/\hat{A}$ is reduced.
8. Density is expressed in terms of animals per unit area, whereas population size simply represents an absolute number of animals.
9. The X matrix does not contain information about capture location. To estimate strip width, and hence density, information concerning the movement of individual animals is obviously required.

Chapter 7

1. It may be logistically easier to use 100 traps for 8 nights. However, using 200 traps for 4 nights may avoid a closure problem and result in increased capture probabilities.
2. Assume that the home range of the animal is circular, and therefore, the radius is 56.4 m. The formula $s \leq (\sqrt{2})\,W$ gives $s \leq 80$ m. For $s \leq W/2$, s should be 28 m. Spacing should be set somewhere within this range, with the actual value depending on the size of the grid and the number of traps available.
3. Model M_{tb} results, and no estimator is available.
4. The probability of capture is likely to vary by occasion (an unwanted source of variation), because one would not expect an animal to have the same capture probability during the day as during the night.

One could pool the morning and evening captures, if time variation is indicated, or analyze them separately, if enough data are available. Checking traps twice daily is certainly preferable to checking only once per day.

5. Closure will be assured.

6. The MODEL SELECTION procedure lacks power, that is, the ability to identify sources of variation in capture probability, when the probabilities of capture are small. In this population, probabilities generally average less than 0.10, and thus Model M_o is selected by default because none of the tests reject any of the hypotheses.

7. The capture probabilities on Tuesday night probably would differ from the remaining occasions, resulting in the presence of time variation. Therefore, the study probably should be continued for at least one more night past the planned termination, to avoid models with time variation. During the analysis, the OCCASIONS= option could be used to eliminate the Tuesday data from model selection and estimation.

Chapter 8

1. a. Geographic closure will be violated. It may be difficult to obtain adequate sample size.
   b. Survival rates and sampling rates may be the only parameters that can be estimated due to the lack of geographic closure.
   c. Catch per unit effort (CPUE) methods, such as *Dupont (1976)*, might be appropriate.
2. Yes. A closed model assumes $S \equiv 1$.
3. Yes. More parameters must be estimated. (See *Cormack 1979:241*.)
4. a. Not necessarily, because the estimators $\hat{S}_j$ and $\hat{N}_j$ have a high sampling correlation as they are computed from the same data.
   b. $cv(\hat{N}_4) = 59/422 = 0.14$ or 14%.
   c. $0.65 \pm 1.96\ (0.04)$ or about 0.57 to 0.73 or 57% to 73%.
   d. Yes, by definition.

5. Yes. At least a good approximation can be computed by taking a weighted average of the annual survival rates; a complex iterative procedure is required due to the covariance structure among the estimators. Alternatively, *Jolly (1979)* provides a model for constant survival rate.