

CHAPTER 7

STUDY DESIGN

This chapter on study design is intended to assist the biologist in performing a capture-recapture study. Because this primer is oriented towards capture-recapture studies of closed populations, the suggestions made here do not always apply to other capture-recapture experiments, such as studies of open populations, or to experiments to estimate survival.

Before a capture-recapture experiment is conducted, the biologist must decide whether this approach is feasible. Other approaches, such as aerial or line transect surveys, may be more appropriate to estimate population size. If only relative differences in population are needed, indirect methods—pellet counts, catch-effort methods, or vegetation damage surveys—may suffice.

Once capture-recapture methods are decided on, the biologist must develop a design to ensure that (1) the assumptions can be tested, (2) the closure assumption is met, (3) the simplest appropriate model is selected from the eight possibilities, and (4) the number of animals captured is maximized (including recaptures). In this chapter, we begin by mentioning livetrapping versus removal methods, then discuss closure, proceed through ways of eliminating variation caused by time, behavior, and heterogeneity, and discuss sample size considerations such as grid size and number of traps.

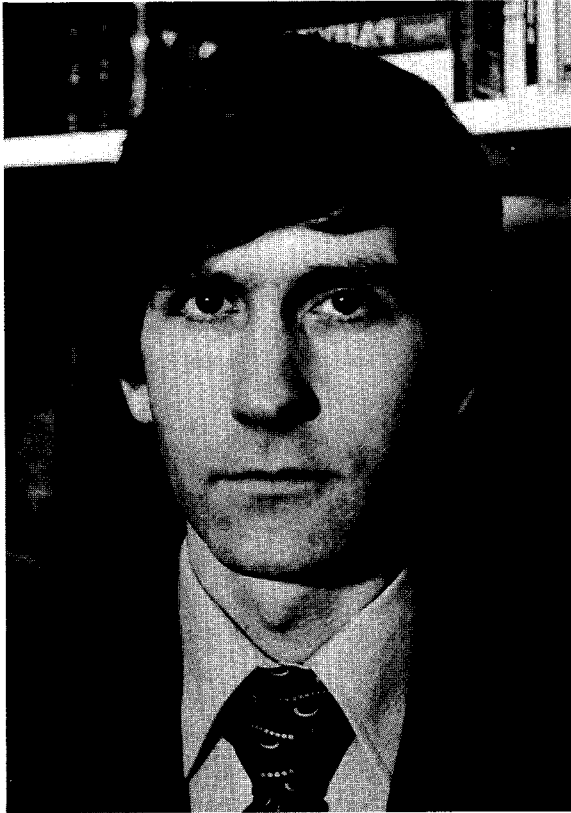
Much of this material is adapted freely from *Otis et al. (1978:74-81)* and *Arnason and Baniuk (1978:180-193)*. For additional discussion of considerations in grid trapping, the reader is referred to *Overton and Davis (1969)*, *M. H. Smith et al. (1969, 1971, 1975)*, *Tanaka (1970)*, and *Hansson (1974)*.

It is beyond the intended scope of this primer to provide guidance on the operational aspects of capture studies, although they are important. For example, if the method of marking (or trapping) is such that marks are lost, a basic assumption needed for meaningful results is violated. If the loss of marks is a significant problem, a double-tagging system can be used to estimate the loss of marks, and the number of unmarked animals in each occasion's sample can be corrected to reflect those that have lost their marks. Others who have worked with the species of interest or with a similar species should be consulted to determine an adequate marking technique. Reviews of marking techniques are given by *Tanner (1978)* and *Southwood (1978)*.

When making decisions about the field study, the biologist should consider the probable effects of the field methods on the subsequent data analysis. Will the field methods provide data that will meet the assumptions of the available data analysis methods? The consequences of the field methods must be evaluated before the data are taken, or the researcher may collect data that will be difficult or impossible to analyze and may generate estimates that will be misleading or absurdly biased. For additional discussion of field procedures, the reader is referred to *Davis (1956)*, *Southwood (1978)*, *Taber and Cowan (1969)*, *Begon (1979)*, and *Tanner (1978)*.

Livetrapping Versus Removal Methods

As discussed in previous chapters, removal methods are a special case of livetrapping methods. That is, the removal estimators can be used on livetrapping data. The marked animals remain in the population, but they are "removed" by being marked. However, the following problems with removal studies suggest that livetrapping methods should be used to maintain design flexibility: (1) removal studies can fail because the estimate is impossible to compute (see Chapter 4), (2) $\text{Var}(\hat{N})$ for removal studies is typically



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Neil Arnason had a head start on the field of biology because both of his parents were entomologists. He studied mathematics and biology as an undergraduate and worked summers at the Statistical Research Service of Canada with E. C. Pielou and L. P. Lefkovich. His Ph.D. degree was taken at the University of Edinburgh under R. M. Cormack. The Statistics Department at Edinburgh had "captured" a large part of the market for people working on capture-recapture theory, and he worked there with G. M. Jolly and R. M. Cormack. His main work was related to the paper J. N. Darroch published in 1961 and focused on estimates of migration in animal populations.

Since leaving Edinburgh in 1970, he has taught modeling and simulation techniques in the Computer Science Department and quantitative ecology in the Zoology Department at the University of Manitoba. Arnason and his colleagues in Winnipeg have developed a comprehensive algorithm for the analysis of data using a variety of open-population methods. He sees the following developments in the future: (1) more powerful model-fitting techniques for capture-recapture data will allow the analyst to fit more specific models to his data; (2) more work will be done to find robust methods; (3) the analysis of capture data to estimate movement and to quantify habitat will be developed beyond its present very primitive state; and (4) new analytic and computational tools will be developed for application to these problems. (Recent photograph by F. Charron.)

greater than $\text{Var}(\hat{N})$ for capture-recapture studies, and (3) the estimate obtained may be totally wrong because a sequence of p_i can be confounded with a constant p . Therefore, we recommend the use of livetrapping methods, if possible, because of the wider array of options available for the data analysis. Removal studies disrupt the population and, as a substantial proportion of the animals is removed, closure-violating immigration may occur.

During livetrapping studies, all possible precautions should be taken to prevent the deaths of animals in the traps, for example, by shading the traps in summer, checking traps more than once a day, shutting them in the afternoon, and avoiding periods of extreme cold. Similarly, it is assumed (implicitly) that the method of marking will not induce mortality. If 20% or greater mortality cannot be avoided, the data must be analyzed as a removal experiment.

Closure

For the analysis methods presented here, the single most important assumption is closure. Testing for closure is very difficult, yet any violation of the assumption biases the tests and population estimators presented here. All closure tests assume M_0 or M_t as the basic underlying model, and therefore, if the data are generated from other models (particularly from M_b), the tests tend to reject the null hypothesis when in fact H_0 is true—a Type I error. Because the tests are poor, we must ensure that the assumption of closure is met.

Methods to help ensure closure include timing the trapping to avoid suspected periods of migration or recruitment, or both, and keeping the experiment as short as possible. For example, when kill traps are

used, animals from the area around the grid will migrate onto the grid as local animals are removed (Gentry *et al.* 1968; M. H. Smith *et al.* 1975:38). The only good solution seems to be to keep the length of the study (in days) very short, so that it will end before significant immigration can occur. If a population must be studied during periods of change, open-population models should be used for data analysis (Seber 1973; Pollock 1975; Arnason and Baniuk 1980).

Eliminating Variation Due to Time, Behavior, and Heterogeneity

If closure is satisfactorily achieved, the next most important considerations are twofold: (1) achieving a number of captures large enough to obtain reliable results, and (2) achieving a study for which the best model is the simplest possible one; for example, Model M_0 rather than M_{tbb} , or Model M_h rather than M_{th} . In this section, we discuss methods of eliminating variation of capture probabilities due to time, behavioral response to first capture, and heterogeneity among individuals.

Of the three factors that affect capture probabilities, time is the most easily controlled by the biologist, but it is the most difficult to handle when present along with other sources of variation. The biologist can select the season of the year when studies are to be conducted, the length of the trapping period, and the time of day when trapping is to be done. In all the decisions, the objective is to reduce variation in capture probabilities over time. Among other things, this means that equal effort should be expended on each occasion, if the methods of this primer are to be used. For example, the number of traps should be the same throughout, trapping should be done at the same times of day, and if bait is used, the type and amount should be the same on all occasions. The study should be done when weather conditions are as constant as possible, because variable weather is likely to cause time variation in capture probabilities (Getz 1961). Arnason and Baniuk (1978) suggest that unequal effort on different trapping occasions may increase effectiveness per unit of effort with open-population models. However, the methods in program CAPTURE will work much more satisfactorily if equal effort results in little variation in capture probabilities due to time.

Behavioral response is common in small mammals, and it is doubtful whether much can be done to avoid it. Apparently for this reason, many biologists have studied and used strict removal methods for small-mammal population estimation. If there is any choice in capture methods for livetrapping, a method that will not result in a trap response should be used. One approach is to use different methods of capture on each occasion (Overton and Davis 1969). Although this procedure may reduce behavioral responses, it also may increase time variation. Because time variation combined with either behavioral response or heterogeneity results in the selection of models with no estimators, the possibility that a procedure may introduce time differences should be considered carefully. The key to reducing time variation is to catch the same number of animals on each occasion; that is, $n_1 \cong n_2 \cong \dots \cong n_t$.

One common source of heterogeneity is the lack of equal access to traps, if the traps are far apart relative to home range (Eberhardt 1969). We recommend the use of four traps per home range.

Other sources of heterogeneity are differences in activity or catchability related to measurable characteristics such as size, age, or sex. These characteristics probably affect an individual's position in the social hierarchy. Such sources can be removed by data stratification, if the characteristics are recorded and if the sample size permits. Data can be stratified to create subsets of the data that are most homogeneous with respect to capture probabilities. This involves nothing more complex than dividing the data into subsets on such variables as species, age, sex, and weight. Unfortunately, sample sizes are seldom large enough to allow stratification. However, if the data are sufficient, the device is valuable. The subsets are analyzed separately by the methods of program CAPTURE. The only additional testing needed might be tests for homogeneity among the strata or subsets (see White 1975).

Heterogeneity due to an unrecognized attribute, such as dominance, cannot be eliminated by stratification. The use of different methods of capture may increase the number of animals captured, but it will not eliminate the basic problem of heterogeneity of capture probabilities.

One possible method of eliminating heterogeneity, and perhaps trap response, is to locate traps randomly on each trapping occasion. Random placement would ensure that, for example, an individual's capture probability would not be consistently high or low because a trap was being placed very near or very far from its den. We are not sure how useful the technique is and would like to see further studies conducted to determine whether it results in significant reductions in heterogeneity. For logistical reasons, the randomization of trap locations on each occasion is probably not very practical, but it may be the only way to eliminate heterogeneity.

A valuable check on the livetrapping methods presented in this primer can be made by using a second method of estimating the proportion of marked animals in the population. A common example is killtrapping or hunting after the capture-recapture experiment has been completed. Then, using the number of marked animals in the population, M_{t+1} , and the ratio of marked to unmarked animals obtained from the killtrapping or hunting, a second and somewhat independent population estimate can be made with *Chapman's (1951)* version of the Lincoln estimator,

$$\hat{N} = \frac{(M_{t+1} + 1) (\text{all animals killtrapped} + 1)}{(\text{marked animals killtrapped} + 1)} - 1 ,$$

(cf. *Seber 1973:60*). Of course, traps are traps, and kill traps still present a strange object in the animal's environment. Another example, for small mammals marked by toe clipping, is to use tracks to obtain a ratio of marked to unmarked animals. Biologists have used tracks on smoked plastic (*Justice 1961*) or on dust-covered tiles to obtain an estimate of the proportion of animals with missing toes and, thus, a second population estimate to compare with the estimate obtained by livetrapping methods. The use of tracks has the distinct advantage of being a truly different method of sampling the population. Confidence in the population estimate is improved when both estimates give similar results.

Sample Size

To obtain reliable estimates of population size, a sufficiently large sample must be taken. Here, "sample size" relates to the number of animals captured and recaptured, not to typical sample-size considerations, such as determining the number of plots to sample. For a livetrapping study, one must have both a large number of distinct animals captured and a sufficient number of recaptures, except for Models M_h and M_{bh} . The factors that control expected numbers of captures are (1) grid size, in terms of area covered and number of traps used; (2) capture probabilities; (3) number of trapping occasions; and (4) population size. We discuss these four factors in relation to the size of the experiment necessary to achieve precise population estimates.

The size of the grid is the first decision to be made. Grid size is a function of trap spacing, and of the number of rows (r) and columns (c) of traps. We suggest equal trap spacing and a systematic grid layout. At each grid station there will be one or more traps. If population densities are very high, we recommend two or more traps per station to avoid competition for traps. However, few studies have been made comparing two or more traps per station with a one-trap station, and further research will be required to determine whether the use of multiple traps per station increases the probability of capture for individual animals.

The objective of grid trapping over a short time period is to estimate the population size and, usually, the density at the grid site. Because of edge effect (discussed in Chapter 5), it is necessary to estimate the effective trapping area as well as N . In practice, this means we must be able to estimate the strip width W , which requires not only that the traps be placed in two dimensions rather than in a single line, but also that each trap can be associated with an X-Y coordinate. For practical reasons, this implies some sort of

regular grid layout, often a square or rectangle, with equal spacing between traps. This aspect of trap layout is not necessary if only N is to be estimated. If the trapping were done on a small island or in an enclosure, for example, knowledge of trap location in a coordinate system would not be needed. Finally, if the density estimate is to be meaningful, the grid should be placed in a homogeneous habitat to ensure nearly uniform density over the grid.

For a choice of r and c when the objective is density estimation, we suggest that both values be greater than or equal to 5; as a minimum we recommend $r + c > 25$. Examples are a square grid 13 by 13 or a rectangle 7 by 20. We note that much work in the literature relies on 16 by 16 grids (*Gentry et al. 1968; M. H. Smith et al. 1971*), and we suggest that grids should be at least that large for the density estimation method based on nested subgrids. We base this recommendation on the fact that a large number of captures is required in each subgrid to achieve a precise estimate; hence, the larger the size of the subgrids, the better the chance that numbers of captures will be large.

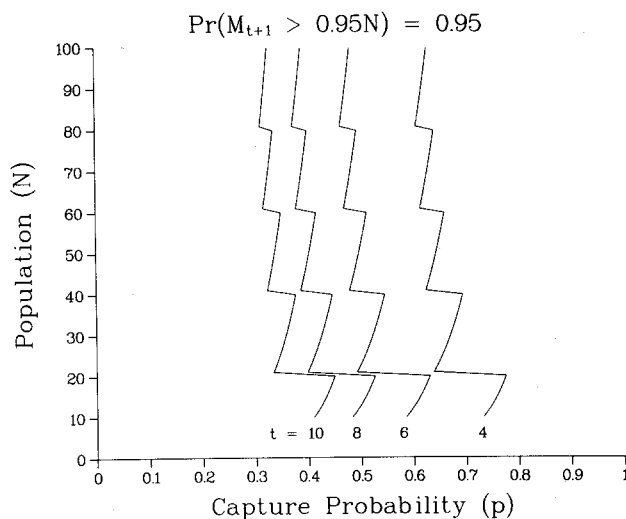
The next decision to be made is the spacing of traps. Most work with small mammals uses 15-m trap spacing or less (*Barbehenn 1974; M. H. Smith et al. 1971*). The rationale, when one is given, relates to the home range size. To illustrate, let s be the spacing between traps, and let $2W$ be the average linear home range size. Home ranges are only rarely circular, but if we assume for design purposes that they are, then the radius here is W . We suggest at least four traps per home range, which implies $s \leq (\sqrt{2})W$. For best results we suggest $s \leq W/2$. Clearly, such a choice implies that some knowledge of home range sizes is needed before a good study can be designed. This requirement is not unreasonable—the biologist should have some behavioral knowledge of the species being studied, so that sampling decisions can be made intelligently. In fact, in any statistical sampling problem, a good study cannot be planned without some prior knowledge of the population parameters to be estimated.

As previously stated, the analyses for estimating population size presented in this primer require a sufficient number of captures to produce satisfactory results. Defining “sufficient numbers” is extremely complicated. Based on our experience with both real and simulated data, however, we have developed some crude guidelines. For instance, experiments in which M_{t+1} is on the order of 10 or 20 animals simply do not provide enough information for any procedure to perform well. The number of different animals captured must be several times larger than 10 or 20, depending heavily on the capture probabilities of the population members being studied. That is, if members’ average capture probabilities are as high as 0.40 or 0.50, program CAPTURE’s estimation and testing methods are useful for a population of about 50, but if the average capture probabilities are only 0.20, the population must be about 200.

In most studies, the number of recaptures must be relatively large before the experiment can produce useful results; again, the magnitude of the number relates to the magnitude of the capture probabilities. In general, the probabilities must be larger for smaller populations, but in no instance should N be less than 20 or average capture probabilities less than 0.30 (for $N < 100$) when trapping occasions are few (say, $t \leq 10$). These recommendations do not guarantee a satisfactory data analysis, but we have seen enough real and simulated data to say that if the data fail these criteria, the achievement of a precise or unbiased estimate is improbable.

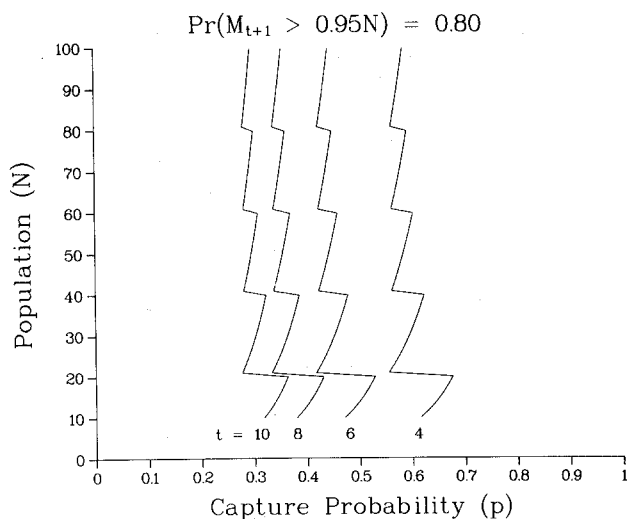
For small population sizes ($N < 100$), we have developed two graphs (*Figs. 7.1, 7.2) to help the biologist determine the number of trapping occasions necessary to catch more than 95% of the population. These figures were developed on the assumption that Model M_0 applies, and they must be used very cautiously, because we do not believe that Model M_0 is applicable to real data. In *Fig. 7.1, the probability that M_{t+1} is greater than 95% of the population is equal to 0.95. In other words, for 95 of 100 experiments, M_{t+1} would exceed 0.95 N . Four values of t are used. From *Fig. 7.1, we conclude that more than 10 trapping occasions are necessary to catch 95% of the population if p is less than about 0.35. Because the assumption of closure is highly suspect for $t > 10$, we conclude that if $N < 100$ and $p < 0.35$, no capture-recapture experiment will provide unbiased and precise estimates. Recall that *Fig. 7.1 assumes Model M_0 , which is an unrealistic model. If the data were actually from Model M_h , the results in *Fig. 7.1 would be too conservative, with an even larger average p required to assume $M_{t+1} > 0.95 N$.

The plot in *Fig. 7.2 is similar to the plot in *Fig. 7.1, but the probability that $M_{t+1} > 0.95 N$ is set at 0.8: that is, 80 of 100 experiments would provide M_{t+1} greater than 95% of N . By comparing the two figures, we see that not much has been gained. The curves are shifted to the left (smaller p), but not drastically. Thus the conclusion still



*Fig. 7.1. Plot of the number of trapping occasions required to catch 95% of the population in 95 of 100 experiments, where $\Pr(M_{t+1} > 0.95N) = 0.95$.

*Fig. 7.2. Plot of the number of trapping occasions required to catch 95% of the population in 80 of 100 experiments, where $\Pr(M_{t+1} > 0.95N) = 0.80$.



remains: if $N < 100$ and $p < 0.3$, a good capture-recapture study probably cannot be done. For $N < 100$, the probability of capture must be in the neighborhood of 0.5.

Estimation of density by nested subgrids requires even larger sample sizes; otherwise the data on the smaller subgrids will be too sparse for reliable results. We believe that reliable density estimates obtained with the subgrid approach require a grid at least 15 by 15 and, as a minimum, a total catch of 75 to 100 different animals.

We now consider an approach to determining a minimum grid area on the basis of these criteria. We start with the relation $N = D A(W)$, where $A(W)$ is the effective trapping area. For a rectangular grid, the relation is

$$N = D [L_r L_c + 2(L_r + L_c) W + \pi W^2] ,$$

where L_r is the length of a row of traps [$L_r = s \times (r - 1)$], and L_c is the length of a column of traps [$L_c = s \times (c - 1)$]. Thus, the area covered by the grid is $L_r L_c$.

Without some knowledge of D and W , we cannot design a suitable study. We assume that D_0 and W_0 are the best guesses of the parameter values. To determine whether a grid study is at all feasible, we set $N = 50$, substitute D_0 and W_0 in the above equation, set $L_r = L_c = L$ (a square grid), and solve for L .

$$L = \sqrt{0.8584(W_0)^2 + N/D_0} - 2W_0 .$$

Although the procedure is not difficult, we must be careful to use the same basic units for D , L , and W . For example, we let W_0 be 150 ft (45.7 m) and assume a density of three animals per acre (7.4 per ha). For compatibility of units, we put D_0 in terms of square feet; then $D_0 = (3/43\,560)$ animals/ft². Solving for L gives

$$L = \sqrt{(0.8584) \times 150^2 + 50 \times 43\,560/3} - 300 = 563 \text{ ft} ,$$

which translates back into 7.3 acres (2.9 ha) as an absolute minimum grid size [$7.3 = (563)^2/43\,560$].

This result is clearly conservative because not all animals will be caught. Improved planning requires that we establish grid size to ensure that a given number of animals M_{t+1} will be caught. But the expected number of different animals that will be caught depends on the true underlying capture probabilities, which are not known. The only practical approach is to make the best guess at the overall average probability of first capture, \bar{p} , applicable during the study and then to use the formula

$$M_{t+1} = N [1 - (1 - \bar{p})^t] .$$

Because the value of t (number of occasions) has been introduced, we can now compute several realistic values of t .

For example, we assume that $\bar{p} = 0.10$, set $M_{t+1} = 50$, and solve for N at several values of t . Given these values of N , we solve for the values of L , and obtain the following minimum grid sizes.

t	N	L	grid size in acres (ha)
4	145	1160	30.9 (12.5)
6	107	952	20.8 (8.4)
8	88	838	16.1 (6.5)

In practice, this example means that, if trapping were only for 4 days, we would need a 9 by 9 grid with traps spaced 150 ft (45.7 m) apart. For an 8-day trapping period, the same (expected) data could be obtained with a 7 by 7 grid with traps spaced 150 ft (45.7 m) apart.

This process can be reversed. Let us say a study is planned with a square grid of 15 traps, spaced 15 m apart ($s = 15$ m). Then, $L_r = L_c = 210$ m. Substitution in the basic equation gives

$$N = D \times [(210)^2 + 2(420)15 + \pi(15)^2] ,$$

$$= D \times 57\,407 \text{ (m}^2\text{)} ,$$

or

$$= D \times 5.74 \text{ (ha)} .$$

If the study is to last 7 days and the average capture probability is about $\bar{p} = 0.15$, then $[(1 - 0.85^7) = (1 - 0.32) = 0.68]$, or

$$M_g = N \times 0.68.$$

For density estimation, we must capture at least 230 animals because the inner 7 by 7 subgrid requires 50; so the density should be large enough that $N \geq 338$ ($338 = 230/0.68$).

$$D \geq 338/5.74 = 58.9 \text{ animals/ha.}$$

Thus, to get reliable results in this study, the true population density should equal or exceed 60 animals per hectare. If the biologist has good reason to believe that true density is only 10 or 20 animals per hectare, the study should be redesigned.

In addition to controlling the sampling effort through the trap spacing and the number of traps, the biologist also can select the number of trapping occasions. In theory, the more trapping times there are, the better will be the results, but this theory ignores the fact that the closure assumption becomes less realistic as more time passes. We recommend a minimum of 5 trapping occasions, but 7 to 10 are better, if closure is assured. The interval between occasions should be short, yet should allow marked individuals to recover from the stress of previous trapping. In practice, most trapping of small animals is done either once a day (morning) or twice a day (morning and evening). Trapping only in the mornings is far less likely to introduce time variation than trapping in the mornings and evenings, when a difference in capture probabilities between times is very likely to occur. If time variation is introduced and variation of behavior and heterogeneity also are present, the correct model will be M_{tth} , for which no suitable estimator is available. Morning and evening trapping may, however, be aimed at different species. Then a workable design would be 5 (or 7) days of trapping in both morning and evening, with separate analyses of the morning and evening data. The possibility also exists of pooling the morning and evening data; pooling the two occasions may increase the probability of capture greatly and, hence, increase the sample size.

In removal studies, the absolute minimum is $t = 3$ occasions (not 2, as is often suggested), because it is impossible to test for equal capture probabilities when $t = 2$. We recommend at least four removals when capture probability is less than 0.5, which is not uncommon (see Chapter 4, Removal Models).

Another valuable method of testing design adequacy before going to the field is to simulate the experiment on a computer with program CAPTURE. Approximate parameter values can be chosen, and the experiment can be replicated as many times as necessary. Among the criteria that can be observed are: the selection of the appropriate model, the bias of the selected estimators, and the achieved confidence level. The validity of the simulations to the field study will necessarily depend on the similarity of the selected parameters to the actual parameter values. A range of parameter values can be simulated, along with a variety of trapping efforts (the number of trapping occasions). Thus cost of the experiment (probably in manpower) can be related to the probable precision of the estimate to be achieved within the range of simulated parameter values. If only unreliable estimates result for the available manpower, the experiment should not be conducted. An excellent discussion of the use of the Monte Carlo simulation to design a study is given by *Arnason and Baniuk (1978:180-193)*.

Unique Identification of Each Captured Animal

In capture-recapture studies, each captured animal is typically given a unique mark. Unique marking systems are preferable in studies where the animals are actually captured and, hence, where the technique is feasible. However, capture-recapture studies often can be performed on animals even when unique marking of each captured individual is not possible. Here, we discuss ways to fulfill the data requirements of all methods presented in this primer except density estimation, without a unique marking system.

The information required to use the model selection procedures discussed in Chapter 3 is that the X_{ij} matrix can be constructed. Each row of the X_{ij} matrix represents the capture history of an animal. No distinction is made

between two animals with the same capture history. Thus the data requirement for construction of the X matrix is that the capture history of each animal can be determined.

An example of the application of a non-unique marking system illustrates the possibilities. Suppose a biologist wants to estimate the number of moose (*Alces alces*) in a particular valley during the winter. Closure can be assumed because snow is deeper on the higher ground surrounding the area than in the valley. Moose are marked from a helicopter with a paint gun. On occasion 1, red paint is used, and 25 moose are given red spots on the rump. On occasion 2, yellow paint is used, and 20 moose are given yellow spots; 15 of these moose already had red spots. Thus after occasion 2, the X matrix would consist of 15 rows of (1,1), 10 rows of (1,0), and 5 rows of (0,1). On occasion 3, orange paint is used, and 22 moose are marked. Of these, 2 had no previous marks, 8 had only red marks, 2 had only yellow marks, and 10 had both yellow and red marks. The resulting X matrix is shown in *Fig. 7.3. Notice that after occasion 1, the matrix consists of only the first 25 rows. After occasion 2, five rows and the second column are added. After occasion 3, two rows and the third column are added; column 3 reflects the

ROW	OCCASION		
	1	2	3
1	1	1	1
2	1	1	1
3	1	1	1
4	1	1	1
5	1	1	1
6	1	1	1
7	1	1	1
8	1	1	1
9	1	1	1
10	1	1	1
11	1	1	0
12	1	1	0
13	1	1	0
14	1	1	0
15	1	1	0
16	1	0	1
17	1	0	1
18	1	0	1
19	1	0	1
20	1	0	1
21	1	0	1
22	1	0	1
23	1	0	1
24	1	0	0
25	1	0	0
26	0	1	1
27	0	1	1
28	0	1	0
29	0	1	0
30	0	1	0
31	0	0	1
32	0	0	1

*Fig. 7.3. The X matrix resulting from the example of marking moose from the air, using a different mark for each occasion.

previous capture histories observed in the field. If the operation were to continue for more occasions, a row for each first capture and a column for each occasion would be added.

One potential problem of the marking scheme described above is that the person marking the animals may select animals already marked (or unmarked). The selection would result in Model M_b because the marker has treated marked animals differently than unmarked animals. This problem is much more difficult if the animals are in a herd, because the smarter or faster animals may disappear before the marker gets a chance to paint them. An example is feral horse herds. As the marker in the helicopter starts singling out animals, the herd may break up, and some animals may escape being marked. On a later occasion, when the same herd is encountered by the helicopter, the same unmarked animals may escape being marked again. Thus, the technique would result in Model M_b , or in Model M_{bh} if the marker showed any selectivity as to which animals were to be marked. Although heterogeneity remains a problem, time variation can be eliminated by marking only on good weather days, and by capturing about the same number of animals each day—that is, by spending the same amount of effort on each occasion.

If a biologist cannot mark animals uniquely or cannot construct an X matrix from the data collected, the model selection procedure cannot be used. It may still be possible to run some of the tests and to calculate most of the estimators on less than the X matrix, but we strongly discourage such practices. Without the application of the model selection procedure to investigate what sort of variation of capture probabilities exists in the data, the biologist is likely to use an estimate from a model that does not fit the data.

Recording Data

In recapture studies, the capture history of each animal caught must be known. Otherwise, substantial information may be lost, and it will be impossible to compute all tests for sources of variation. Although it may seem obvious, we insist that recording all data (animal numbers and trap locations) correctly is crucial.

If density is to be estimated on the basis of grid trapping data, trapping location also must be recorded. The minimum information that must be taken when a capture occurs includes the animal identification code and the trapping occasion. Usually, the species, sex, and age also are recorded for each animal, although for the analyses given here the only purpose is to enable subsequent partitioning of the data. We recommend analyzing the data separately by species, but often data are too few to be partitioned by sex and age.

For true removal studies, like electrofishing, there is no animal identification code. As suggested by *Raleigh and Short (1981)*, recording each individual by species and analyzing the data at least by major taxonomic groups are both very important in removal studies.

To know the trap location, traps must be numbered uniquely. Moreover, the biologist must know the relation between the trap number and its coordinate on some arbitrary rectangular X-Y coordinates. We strongly recommend use of this system, and we stress that density estimation with program CAPTURE requires that data be collected in this context. The northwest corner trap should be numbered (1,1), because (0,0) indicates no capture in the program CAPTURE code. Then the rows become the X-axis and the columns the Y-axis. For example, a 10 by 10 grid would look like Fig. 7.4. This system can be extended to cover any rectangular grid of rows and columns.

When traps are checked both morning and evening, it is necessary to record both the day and the time of capture. The data can be analyzed as two occasions per day, or they can be pooled as one occasion.

Standard field forms and standard conventions for trap numbering and animal identification facilitate data recording. One example of a standardized method is presented in *Brotzman and Giles (1966)*. Figure 7.5 shows a keypunch field form that is compatible with program CAPTURE. We recommend recording data directly on a keypunch form to avoid errors in transcribing the data from field notebooks. Keypunch forms can be duplicated for field use.

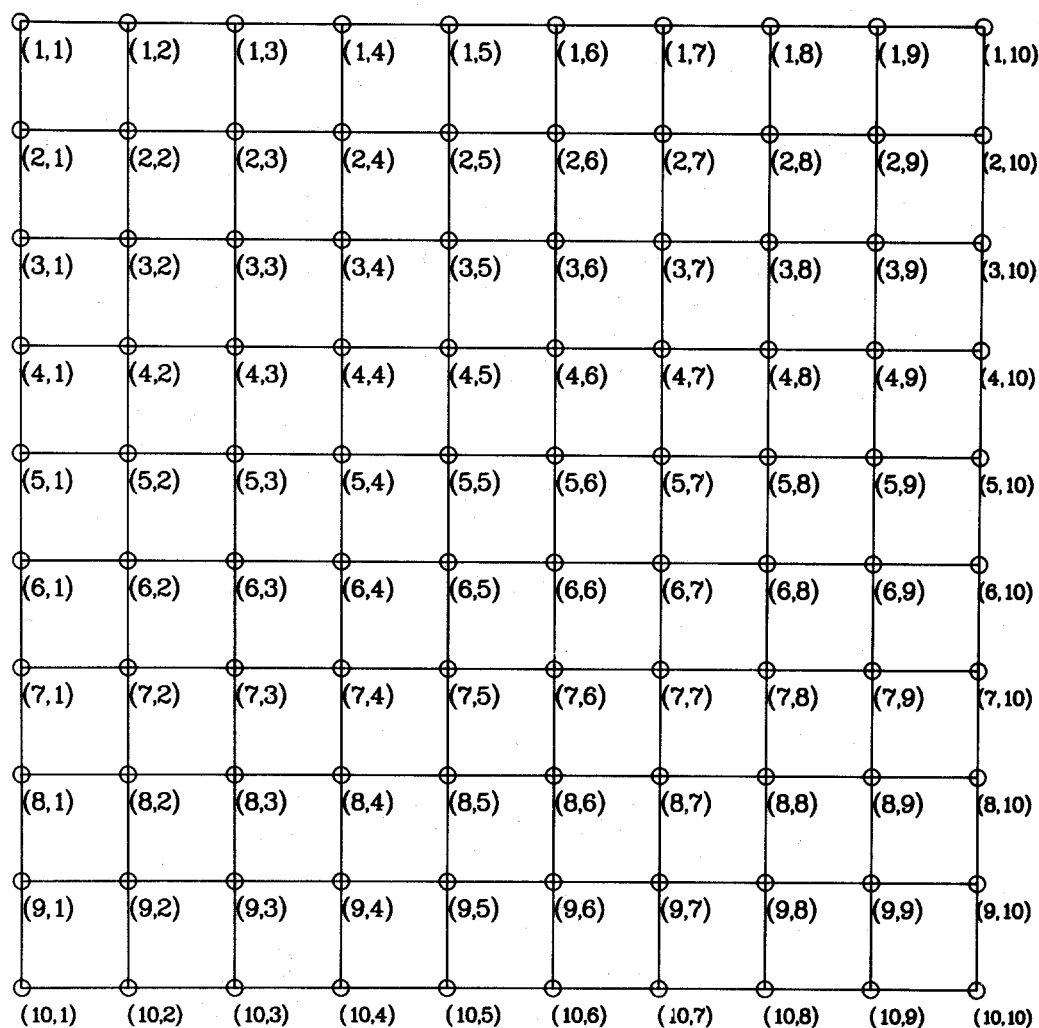


Fig. 7.4. The coordinates represent the trap numbering system used by program CAPTURE. The upper left (northwest) trap is labeled (1,1) *not* (0,0), because zero coordinates would indicate that the animal was not caught on that occasion.

Data Anomalies

Various anomalies and unplanned events may occur during trapping. For example, (1) several animals may be found in one trap, (2) animals may be found dead in traps; (3) animals that have been released may be found further down the grid, trapped again on the same occasion; and (4) a trapped animal may escape when it is removed from the trap. We make the following suggestions regarding these happenings.

(1) More than one animal per trap presents no problem; each animal is recorded separately. This type of data does not invalidate the analyses presented here.

(2) A dead animal in a trap in a livetrapping study is a more serious problem. On the last trapping occasion, the dead animal does not matter; the capture is recorded as normal. Otherwise, the data analysis must be modified. Some of the methods described here (specifically, Models M_0 and M_1) can allow for known removals in a true livetrapping study. Because not all tests and estimators can be modified, we have not dealt here with such models. We recommend the following: if trap deaths are less than 5% of total captures, remove the dead-animal data from the total results, run the analyses, add the number of dead animals to \hat{N} , and then multiply the density estimate \hat{D} by $(1 + \text{proportion dead})$. If trap deaths are more than 20% of total captures, use the generalized removal method of analysis on first capture. For 5-20% trap deaths, the only "safe" analysis may be the removal method, although

ID	SPECIES		CAPTURE 1		CAPTURE 2		CAPTURE 3		CAPTURE 4		CAPTURE 5		CAPTURE 6		CAPTURE 7		CAPTURE 8		CAPTURE 9		CAPTURE 10		CAPTURE 11		CAPTURE 12		
	t	x	y	t	x	y	t	x	y	t	x	y	t	x	y	t	x	y	t	x	y	t	x	y	t	x	y
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Fig. 7.5. A computer form for recording capture histories for input to program CAPTURE. The TASK cards (Appendix A) to read this data form would be
 TASK READ CAPTURES XY REDUCED OCCASIONS=12
 FORMAT=(A3,5X,36 (F2.0)).

deletion of the dead animals may be preferable if the loss of information can be afforded. These modifications give \hat{N} and \hat{D} relative to the first day of the study. To make these estimates apply to the population remaining alive after the study, simply delete all trap deaths from the data set before analysis.

(3) When the same animal is caught more than once on a given occasion, the only added information provided is on movement. We recommend that both captures be recorded, but that only the results of the first capture be used for data analysis.

(4) When an animal escapes during handling before it is tagged, or before the mark is read, do nothing. In essence, this animal does not become part of the data.

Simulation Example

To illustrate the use of Monte Carlo simulation for design of a capture-recapture experiment, we use the data from E. Larsen given in *Otis et al. (1978:42-43)*. The same data set is provided with program CAPTURE, so the reader can duplicate the following computer results.

Great Basin pocket mice (*Perognathus parvus*) were livetrapped in a desert community in Curlew Valley, Utah, during June 1977. The data are from 7 consecutive nights of livetrapping, with traps arranged in a 12 by 12 grid and spaced 15 m apart. The model selection procedure selected either Model M_{tth} or Model M_{bth} as appropriate for use in estimating N . The data on model selection and the results of using \hat{N}_{bth} to produce point and interval estimates of N are given in *Fig. 7.6.

Note that the confidence interval for N in *Fig. 7.6 is quite large. If we want to repeat the study, how should we modify it to obtain a confidence interval smaller than $\pm 20\%$ of \hat{N} , assuming field conditions have not changed drastically?

From *Fig. 7.6, we see that the estimate used there came from a model with two average capture probabilities: about 0.3 and 0.14. On the first trapping occasion, 23 animals were caught and $\bar{p}_1 = 0.3$, so the population must have consisted of a fair number of animals with large capture probabilities. If we assume that $N = 77$, the animals left uncaught had a mean capture probability of 0.15. Thus we might model the capture probabilities of the population as

Number of Animals	Capture Probability
20	0.10
20	0.20
37	0.65

We determined these numbers in a crude fashion by simulating various combinations until we obtained data and results similar to those of *Fig. 7.6.

We first simulate the Larsen experiment from June 1977 to see whether the results from the hypothetical capture probabilities are consistent with the observed data. The input to program CAPTURE is as follows.

```
TASK SIMULATE POPULATION=77 OCCASIONS=7 REPLICATIONS=100
HETEROGENEITY=20,0.1,20,0.2,37,0.65
BEHAVIOR=77,1.4
```

The BEHAVIOR card guarantees that trap response is present, and thus that M_{bth} is the true underlying model for the simulated data. From the summary of the simulation results presented in *Fig. 7.7, we note that Model M_{tth} was never selected, yet the model selection procedure output in *Fig. 7.6 indicates that M_{tth} is just as likely to occur as M_{bth} . Another indication that the simulations are not realistic representations of the situation is the width of the confidence interval for the generalized removal estimator: the average confidence interval width in the simulations is about 11, whereas the confidence interval width for Larsen's data is 98. Other sets of parameters for Model M_{bth} likewise do not appear to provide a reasonable representation of the real data. The reader may try other parameter sets for Model M_{bth} to duplicate Larsen's data.

MODEL SELECTION PROCEDURE. SEE MODEL SELECTION SECTION OF THE MONOGRAPH FOR DETAILS.
DATA FROM E. LARSEN, PEROGNATHUS PARVUS, CURLEW VALLEY, UTAH.

OCCASION	J=	1	2	3	4	5	6	7
ANIMALS CAUGHT	N(J)=	23	22	17	17	22	25	34
TOTAL CAUGHT	M(J)=	0	23	32	35	40	46	55
NEWLY CAUGHT	U(J)=	23	9	3	5	6	6	3
FREQUENCIES	F(J)=	16	15	6	5	5	5	3

1. TEST FOR HETEROGENEITY OF TRAPPING PROBABILITIES IN POPULATION.
NULL HYPOTHESIS OF MODEL M(O) VS. ALTERNATE HYPOTHESIS OF MODEL M(H)

CHI-SQUARE VALUE = 61.688 DEGREES OF FREEDOM = 4 PROBABILITY OF LARGER VALUE = 0.00000

2. TEST FOR BEHAVIORAL RESPONSE AFTER INITIAL CAPTURE.
NULL HYPOTHESIS OF MODEL M(O) VS. ALTERNATE HYPOTHESIS OF MODEL M(B)

CHI-SQUARE VALUE = 7.844 DEGREES OF FREEDOM = 1 PROBABILITY OF LARGER VALUE = 0.00510

3. TEST FOR TIME SPECIFIC VARIATION IN TRAPPING PROBABILITIES.
NULL HYPOTHESIS OF MODEL M(O) VS. ALTERNATE HYPOTHESIS OF MODEL M(T)

CHI-SQUARE VALUE = 15.596 DEGREES OF FREEDOM = 6 PROBABILITY OF LARGER VALUE = 0.01609

4. GOODNESS OF FIT TEST OF MODEL M(H)
NULL HYPOTHESIS OF MODEL M(H) VS. ALTERNATE HYPOTHESIS OF NOT MODEL M(H)

CHI-SQUARE VALUE = 18.236 DEGREES OF FREEDOM = 6 PROBABILITY OF LARGER VALUE = 0.00567

TEST OF MODEL M(H) BY FREQUENCY OF CAPTURE
(FREQUENCIES LESS THAN 21 ARE NOT CALCULATED.)

NUMBER OF CAPTURES CHI-SQUARE D.F. PROBABILITY

1	5.000	6	0.54381
2	22.240	6	0.00110

MODEL SELECTION PROCEDURE. SEE MODEL SELECTION SECTION OF THE MONOGRAPH FOR DETAILS.
DATA FROM E. LARSEN, PEROGNATHUS PARVUS, CURLEW VALLEY, UTAH.

5. GOODNESS OF FIT TEST OF MODEL M(B)
NULL HYPOTHESIS OF MODEL M(B) VS. ALTERNATE HYPOTHESIS OF NOT MODEL M(B)

CHI-SQUARE VALUE = 17.856 DEGREES OF FREEDOM = 10 PROBABILITY OF LARGER VALUE = 0.05743

- 5A. CONTRIBUTION OF TEST OF HOMOGENEITY OF FIRST CAPTURE PROBABILITY ACROSS TIME

CHI-SQUARE VALUE = 9.966 DEGREES OF FREEDOM = 5 PROBABILITY OF LARGER VALUE = 0.07622

- 5B. CONTRIBUTION OF TEST OF HOMOGENEITY OF RECAPTURE PROBABILITIES ACROSS TIME

CHI-SQUARE VALUE = 7.891 DEGREES OF FREEDOM = 5 PROBABILITY OF LARGER VALUE = 0.16235

6. GOODNESS OF FIT TEST OF MODEL M(T)
NULL HYPOTHESIS OF MODEL M(T) VS. ALTERNATE HYPOTHESIS OF NOT MODEL M(T)

CHI-SQUARE VALUE = 60.390 DEGREES OF FREEDOM = 22 PROBABILITY OF LARGER VALUE = 0.00002

7. TEST FOR BEHAVIORAL RESPONSE IN PRESENCE OF HETEROGENEITY.
NULL HYPOTHESIS OF MODEL M(H) VS. ALTERNATE HYPOTHESIS OF MODEL M(BH)

CHI-SQUARE VALUE = 17.988 DEGREES OF FREEDOM = 14 PROBABILITY OF LARGER VALUE = 0.20731

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	0.80	0.86	0.62	0.99	0.00	0.59	0.54	1.00

APPROPRIATE MODEL PROBABLY IS M(TBH) OR M(BH)
SUGGESTED ESTIMATOR IS GENERALIZED REMOVAL.

*Fig. 7.6. Analysis from program CAPTURE of Larsen's data on pocket mice in Curlew Valley, Utah.

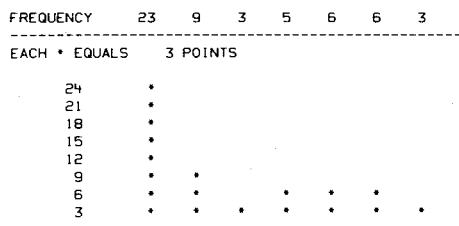
POPULATION ESTIMATION WITH VARIABLE PROBABILITY REMOVAL ESTIMATOR. SEE M(BH) OR REMOVAL MODELS OF THE MONOGRAPH FOR DETAILS.
 DATA FROM E. LARSEN, PEROGNATHUS PARVUS, CURLEW VALLEY, UTAH.

OCCASION	J=	1	2	3	4	5	6	7
TOTAL CAUGHT	M(J)=	0	23	32	35	40	46	52
NEWLY CAUGHT	U(J)=	23	9	3	5	6	6	3

K	N-HAT	SE(N)	CHI-SQ.	PROB.	ESTIMATED P-BAR(J), J=1, ..., 7							
1	60.61	4.456394	9.965	0.0762	0.2802	0.2802	0.2802	0.2802	0.2802	0.2802	0.2802	
2	76.73	24.66909	3.486	0.4801	0.2998	0.1377	0.1377	0.1377	0.1377	0.1377	0.1377	
3	FAILURE CRITERION = -2 NO ESTIMATES FOR THIS STEP.											
4	67.44	18.18989	1.308	0.5201	0.3410	0.2025	0.0846	0.2067	0.2067	0.2067	0.2067	
5	58.65	5.896785	0.823	0.3643	0.3922	0.2525	0.1126	0.2114	0.3953	0.3953	0.3953	

POPULATION ESTIMATE IS 77 WITH STANDARD ERROR 24.6691
 APPROXIMATE 95 PERCENT CONFIDENCE INTERVAL 28 TO 126

HISTOGRAM OF U(J)



*Fig. 7.6 (cont.)

Because of the contrast between the real and simulated data, we constructed a more complex set of capture probabilities from M_{bh} . The input to program CAPTURE is as follows.

TASK SIMULATE POPULATION=77 OCCASIONS=7 REPLICATIONS=100
 HETEROGENEITY=30,0.3,30,0.5,17,.90
 BEHAVIOR=77,1.4
 TIME=0.6,0.6,0.5,0.5,0.6,0.6,0.7

As seen in *Fig. 7.8, the simulation output appears comparable to the results of Larsen. Two major differences are noted between the output in the two figures: in *Fig. 7.8, the confidence interval width for M_{bh} is greatly expanded, and the average estimate for M_{bh} appears to be less biased. These two differences cause appreciably better coverage for the M_{bh} results—84% in *Fig. 7.8 as opposed to 15% in *Fig. 7.7.

What conclusions can we base on these simulations? We suggest that, if the study were to be redone, the variation in capture probabilities through time should be eliminated if any kind of precision is to be achieved. The estimates in *Fig. 7.8 are accurate, but the precision is so poor that the investigator could have no confidence in the estimate. If a true Model M_{bh} data set were obtained, the estimate would be precise (although biased). However, the investigator, having access to the simulation results in *Otis et al. (1978:130)*, realizes that the generalized removal estimator typically is biased low. Even though a precise wrong answer is obtained, the investigator is aware of this fact and can correct for the bias on the basis of the simulation in *Otis et al. (1978)*, plus any additional simulations he may undertake. However, this approach should be documented carefully to enable other researchers to verify the results; in fact, the “doctoring” of an estimate should be avoided.

DATA SIMULATION PROCEDURE. SEE FIELD PROCEDURES SECTION OF THE MONOGRAPH FOR DETAILS.

RANDOM SEED IS 1234567

NUMBER OF REPLICATIONS 100

NUMBER OF OCCASIONS 7

NUMBER IN POPULATION 77

HETEROGENEITY STRUCTURE

NUMBER VALUE

20 0.100
 20 0.200
 37 0.650

TIME VARIATION STRUCTURE

NUMBER VALUE

1 1.000
 2 1.000
 3 1.000
 4 1.000
 5 1.000
 6 1.000
 7 1.000

BEHAVIOR STRUCTURE

NUMBER VALUE

77 1.400

DATA SIMULATION PROCEDURE. SEE FIELD PROCEDURES SECTION OF THE MONOGRAPH FOR DETAILS.

MODEL SELECTION RESULTS

MODEL	TIMES SELECTED	PERCENT	FAILURES	AVERAGE	STANDARD ERROR	LCI	UCI
POINT ESTIMATES							
M(O)	0	0.000	0	0.00	0.0000	0.0	0.0
M(H)	23	23.000	0	77.00	2.7111	71.4	82.6
M(B)	31	31.000	0	63.55	0.5881	62.4	64.7
M(BH)	33	33.000	0	64.88	0.7843	63.3	66.4
M(T)	0	0.000	0	0.00	0.0000	0.0	0.0
M(TH)	1	1.000	0	0.00	0.0000	0.0	0.0
M(TB)	9	9.000	0	0.00	0.0000	0.0	0.0
M(TBH)	3	3.000	0	0.00	0.0000	0.0	0.0

INTERVAL ESTIMATE LENGTHS COVERAGE PERCENT

M(O)	0	0.000	0	0.00	0.0000	0.0	0.0
M(H)	12	52.174	0	20.19	2.6614	14.7	25.7
M(B)	0	0.000	0	6.73	0.3946	6.0	7.5
M(BH)	5	15.152	0	10.82	1.8982	7.1	14.5
M(T)	0	0.000	0	0.00	0.0000	0.0	0.0
M(TH)	0	0.000	0	0.00	0.0000	0.0	0.0
M(TB)	0	0.000	0	0.00	0.0000	0.0	0.0
M(TBH)	0	0.000	0	0.00	0.0000	0.0	0.0

TEST SIZE RESULTS

TEST		0.01	0.05	0.10
M(O) VS. M(H)		0.01	0.01	0.01
M(O) VS. M(B)		0.98	1.00	1.00
M(O) VS. M(T)		0.13	0.35	0.45
M(H) VS. NOT M(H)		0.44	0.58	0.70
M(B) VS. NOT M(B)		0.07	0.19	0.31
M(T) VS. NOT M(T)		0.99	0.99	0.99
M(H) VS. M(BH)		0.61	0.77	0.85
CLOSURE		0.30	0.57	0.73

*Fig. 7.7. Program CAPTURE simulation output to duplicate Larsen's 1977 data. On this first attempt, only heterogeneity and behavioral response are included.

DATA SIMULATION PROCEDURE. SEE FIELD PROCEDURES SECTION OF THE MONOGRAPH FOR DETAILS.

RANDOM SEED IS 1234567

NUMBER OF REPLICATIONS 100

NUMBER OF OCCASIONS 7

NUMBER IN POPULATION 77

HETEROGENEITY STRUCTURE

NUMBER	VALUE
30	0.300
30	0.500
17	0.900

TIME VARIATION STRUCTURE

NUMBER	VALUE
1	0.600
2	0.600
3	0.500
4	0.500
5	0.600
6	0.600
7	0.700

BEHAVIOR STRUCTURE

NUMBER	VALUE
77	1.400

DATA SIMULATION PROCEDURE. SEE FIELD PROCEDURES SECTION OF THE MONOGRAPH FOR DETAILS.

MODEL SELECTION RESULTS

MODEL	TIMES SELECTED	PERCENT FAILURES	AVERAGE	STANDARD ERROR	LCI	UCI

POINT ESTIMATES						
M(O)	0	0.000	0	0.00	0.0000	0.0
M(H)	21	21.000	0	77.79	1.3300	75.0
M(B)	20	20.000	0	73.95	1.3128	71.2
M(BH)	43	43.000	0	80.93	3.9741	73.1
M(T)	0	0.000	0	0.00	0.0000	0.0
M(TH)	2	2.000	0	0.00	0.0000	0.0
M(TB)	1	1.000	0	0.00	0.0000	0.0
M(TBH)	13	13.000	0	0.00	0.0000	0.0

INTERVAL ESTIMATE LENGTHS						
	COVERAGE	PERCENT				

M(O)	0	0.000	0	0.00	0.0000	0.0
M(H)	18	85.714	0	17.10	0.9393	15.1
M(B)	17	85.000	0	26.28	2.1869	21.7
M(BH)	36	83.721	0	83.49	40.7797	3.6
M(T)	0	0.000	0	0.00	0.0000	0.0
M(TH)	0	0.000	0	0.00	0.0000	0.0
M(TB)	0	0.000	0	0.00	0.0000	0.0
M(TBH)	0	0.000	0	0.00	0.0000	0.0

TEST SIZE RESULTS

TEST	0.01	0.05	0.10

M(O) VS. M(H)	0.87	0.95	0.96
M(O) VS. M(B)	0.65	0.83	0.88
M(O) VS. M(T)	0.36	0.64	0.75
M(H) VS. NOT M(H)	0.42	0.69	0.79
M(B) VS. NOT M(B)	0.04	0.20	0.27
M(T) VS. NOT M(T)	0.50	0.66	0.76
M(H) VS. M(BH)	0.17	0.37	0.53
CLOSURE	0.00	0.05	0.11

*Fig. 7.8. The second attempt at simulating Larsen's data, by using Model M_{tbh} .

Check List

To summarize this chapter, we have prepared a brief check list of questions to be answered before a capture-recapture study is started.

1. Is a better approach available than the capture-recapture method? For example, line transect surveys?
2. Is a closed population being considered?
3. Is a reliable marking procedure available?
4. Will the data be fit by a model with an estimator? Stated differently, given that heterogeneity of capture probabilities may be assumed to exist, can time variation be eliminated to give Model M_{bh} or Model M_h ?
5. How precise an estimate is needed from the study?
6. Are the manpower and resources available to obtain the necessary precision?

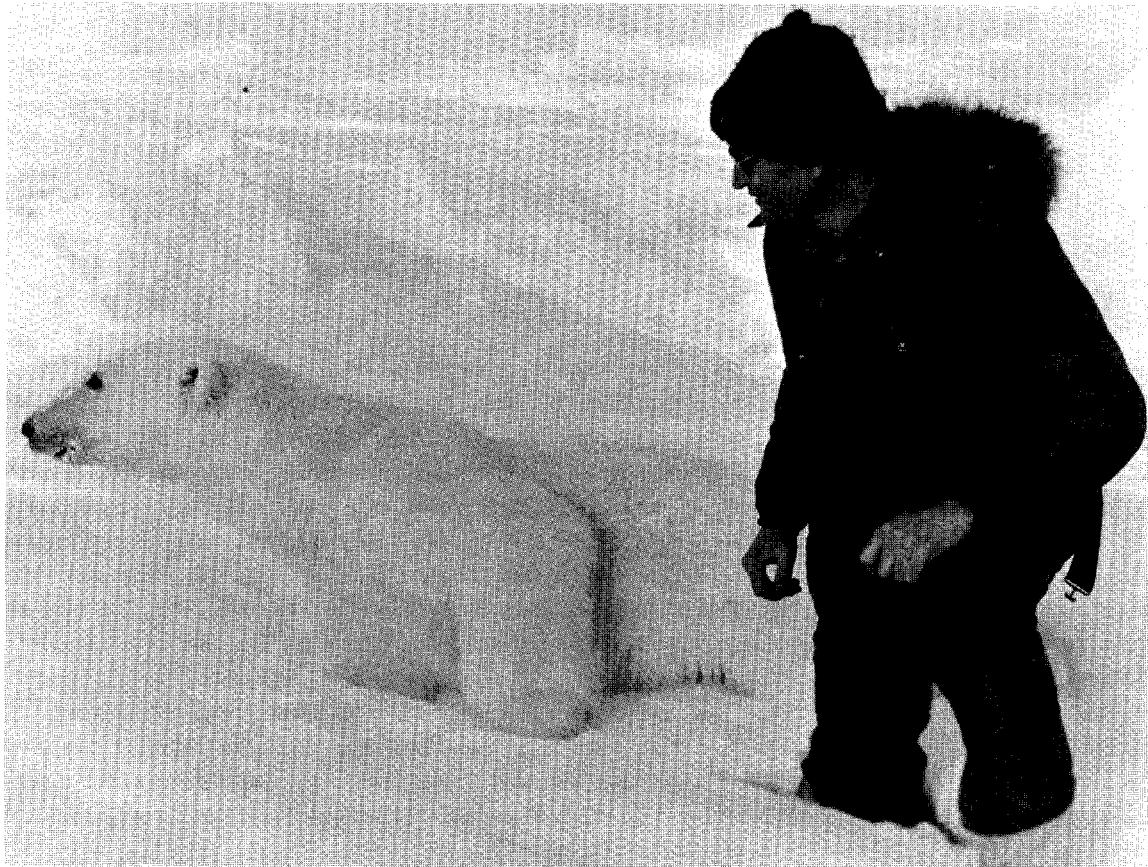
Questions and Exercises

1. Compare the advantages and disadvantages of using 100 traps for 8 nights versus 200 traps for 4 nights to trap meadow voles (*Microtus pennsylvanicus*) in an old field. Assume that the grid size for both experiments is the same.
2. Assume that you know the home range of an animal is 10 000 m². What trap spacing would you use?
3. What are the disadvantages if both time and behavior influence capture probabilities?
4. Comment on a capture-recapture experiment in which traps are checked morning and evening. What problems might you encounter? Would you pool the data?
5. What is the advantage of fencing the ends of a stream segment where you will conduct an electrofishing experiment?
6. The following input to program CAPTURE was used to simulate a capture-recapture experiment.

```
TASK READ CAPTURES POPULATION=50 OCCASIONS=4
HETEROGENEITY=20,0.05,10,0.10,20,0.15
TIME=1.0,1.5,1.0,0.5
BEHAVIOR=50,0.5
```

The data are obviously from Model M_{tth} , yet the results from CAPTURE indicate that more than 90% of the time, Model M_0 is selected. Why? (Hint: What is the average probability of capture on each occasion?)

7. You are doing a 5-night small-mammal capture-recapture study starting on Monday. On Tuesday night, the weather turns much colder with rain, but by Wednesday morning weather conditions have returned to normal. What problems would you expect when you analyze the data? What might you consider to rectify these problems, both during the remainder of the trapping sessions and later, during the analysis?



Tagging large animals like polar bears does not fit the methods in this primer because too few animals are recaptured, and the studies are generally long-term; that is, they are better modeled by open-population models. (Photograph courtesy of Jack Lentfer.)



Population estimates of medium-sized mammals such as this raccoon (*Procyon lotor*) may be made with capture-recapture methods, but often capture probabilities are small, and animals are not recaptured, making the methods in this primer inappropriate. (Photograph courtesy of Alan Sargeant and Raymond Greenwood.)



The use of radio collars on big game, such as elk (*Cervus elaphus*), does not generally provide reliable capture-recapture estimates unless recaptures are obtained through other methods, such as aerial observations of the collars (see Rice and Harder 1977). Survival rates can be obtained from biotelemetry data. (Photograph courtesy of Kenneth V. Bostick.)