CHAPTER 6
EXAMPLES

When the reader has become familiar with the concepts presented in Chapters 2 to 5, he will need some experience in their application. In this chapter, we provide an opportunity to perform extensive analysis of several examples. We have included annotated computer output so that the reader can become familiar with the output from program CAPTURE, although in some cases only the output relevant to the particular example has been included.

Note that notation in the computer output differs from notation in the text, because most computer printers cannot provide subscripts. Thus, for example, the text notation M_t corresponds to the computer notation M(T). Parentheses are used to denote subscripts. Additional examples can be found in *Otis et al. (1978:81-96).*

Example 1. Interpreting the Data

For this example, we have created a series of simulated experiments to help the reader develop insight into the catchability structure of the population under study by examining some key summary statistics of the capture data. In all of these experiments, the population size is 300 and there are 7 trapping occasions.

Figure 6.1a gives the summary statistics for a population having no variation in capture probabilities among its members (Model M_o, $p = 0.20$). The most significant aspect of the statistics is that there is nothing unusual about them: daily captures remain relatively constant and the frequencies of capture show a steady decline. Contrast this vector of frequencies with those displayed in Fig. 6.1b. The statistics in Fig. 6.1b were generated from a heterogeneous population of individuals in which 3 groups of 100 animals have capture probabilities equal to 0.1, 0.2, and 0.3, respectively (Model M_h). Many more animals have been caught three or more times in this experiment than in the previous one; the increase indicates that some members of the population are very susceptible to trapping. Indeed, nearly 35% of the animals captured are captured more than twice, as opposed to only 15% in the M_o experiment. Also, the daily captures have remained relatively stable. Thus, the best clue the researcher has for detecting heterogeneity arises from irregularities in the frequencies of capture. As we shall see below, other sources of unequal catchability tend to produce more obvious changes in the statistics than does individual heterogeneity.

CHAPTER 6 M(O) PART OF M(TBH) EXAMPLE 1

OCCASION	J=	1	2	3	4	5	6	7	
ANIMALS CAUGHT	N(J)=	58	58	61	66	61	57	51	
TOTAL CAUGHT	M(J)=	0	58	104	146	175	205	229	240
NEWLY CAUGHT	U(J)=	58	46	42	29	30	24	11	
FREQUENCIES	F(J)=	115	89	27	7	2	0	0	

Only 36 animals were captured more than twice in 7 occasions

Daily captures are fairly constant

CHAPTER 6 M(H) PART OF M(TBH) EXAMPLE 1

OCCASION	J=	1	2	3	4	5	6	7	
ANIMALS CAUGHT	N(J)=	60	66	59	57	57	48	67	
TOTAL CAUGHT	M(J)=	0	60	108	143	166	180	194	211
NEWLY CAUGHT	U(J)=	60	48	35	23	14	14	17	
FREQUENCIES	F(J)=	97	55	37	16	4	2	0	

During the course of the experiment 59 animals were captured more than twice

Figure 6.1c contains statistics generated from trapping a population with the heterogeneity structure described in the M_h experiment and an added factor: the overall trapping success on the first two occasions was roughly 25% greater than that experienced on the remaining five occasions. Thus, the probability structure of this population corresponds to Model M_{th}. The time factor has caused a much larger number of captures on the first two occasions relative to the other occasions. A large variation of this type among the total animals caught on each occasion is the best indicator that time variation is playing a role. Again, the percentage of animals captured more than twice is large (almost 30%), as was the case in Fig. 6.1b.

Finally, consider the statistics presented in Fig. 6.1d. The most interesting feature of these data is that the daily captures exhibit a U-shape—that is, the number of animals caught starts out high, gradually declines, and then gradually builds up again, peaking on the last occasion. This pattern is caused by the addition of a behavioral response in the population to the same sources of unequal catchability (heterogeneity and time variation) contained in the previous population. (Animals have a 30% greater chance of recapture than of first capture; they become trap happy.) Thus, we are dealing with a population in which all three sources of unequal catchability are operating (Model M_{tbh}). As before, the large number of first captures is caused by a greater overall trapping success (time variation) on those occasions. The gradual buildup in the number of animals caught beginning on the fifth occasion is caused by the trap happiness of the population. That is, after an animal is caught, it has a 30% greater chance of being recaptured; thus, as more and more individuals are caught, the overall susceptibility of the population to trapping increases, and more and more individuals are caught. Of course, the variation among daily captures could have been caused by time variation alone. However, the fact that captures show a steady increase with time is a signal that perhaps behavioral variation is responsible. Conversely, we might suspect that animals were trap shy if captures showed a steady decline from some relatively constant level.

This series of experiments represents only a sample of the literally infinite number of situations that can arise in the real world. The reader must think about what kinds of probability structure could be causing the pattern discerned in the statistics generated by the experiment. The potential complexity of the probability structures of real data necessitates rigorous testing of the data; this testing is the function of the model selection procedure in program CAPTURE.

There is a big drop in capture success after the second occasion

CHAPTER 6 M(TH) PART OF M(TBH) EXAMPLE 1

OCCASION	J=	1	2	3	4	5	6	7	
ANIMALS CAUGHT	N(J)=	82	84	59	57	57	48	67	
TOTAL CAUGHT	M(J)=	0	82	135	166	186	199	210	225
NEWLY CAUGHT	U(J)=	82	53	31	20	13	11	15	
FREQUENCIES	F(J)=	98	61	42	14	8	2	0	

Fig. 6.1c. The summary statistics from a simulated experiment on a Model M_{th} population.

Because heterogeneity is still present many animals are captured more than twice

CHAPTER 6 M(TBH) PART OF M(TBH) EXAMPLE 1

OCCASION	J=	1	2	3	4	5	6	7	
ANIMALS CAUGHT	N(J)=	82	80	70	70	73	83	95	
TOTAL CAUGHT	M(J)=	0	82	128	158	191	210	228	241
NEWLY CAUGHT	U(J)=	82	46	30	33	19	18	13	
FREQUENCIES	F(J)=	73	77	54	22	14	1	0	

Fig. 6.1d. The summary statistics from a simulated experiment on a Model M_{tbh} population.

The effects of behavioral response on daily captures appear in the last few occasions

Example 2. Trap Happy or Trap Shy—No Difference?

In a Florida sugar cane field, 76 traps were placed along 6 parallel transects and baited with apples. Traps were placed 15.4 m apart on a transect, transects were an average 80 m apart, and trapping was done for 8 consecutive days. The species under study was the cotton rat (*Sigmodon hispidus*). Trapping results are summarized in Fig. 6.2a. The model selected as appropriate for population estimation was the behavioral response Model M_b (Fig. 6.2b). The results given in Fig. 6.2c show that the rats evidently are becoming trap happy—the probability of recapture is 0.38 as opposed to 0.23 for first capture. To illustrate a point, we manipulated this data set so that the sequence of newly captured animals remains unchanged, but rats now tend to avoid recapture (Fig. 6.2d). The model selection procedure still selects the behavioral model as appropriate, and the population estimation results are as given in Fig. 6.2e. The probability of first capture is the same as before (0.23), but now probability of recapture is 0.07. The population estimate and its estimated standard error, however, remain the same! The lack of change in the estimate illustrates the point that, in behavioral response models, recaptures have no effect on the bias or precision of the estimate. This fact should affect construction of the study design if, on the basis of previous knowledge, the researcher has decided that the behavioral response model probably will be used to analyze the data. See Chapter 7 (Study Design) for a discussion of ways to make such a priori decisions. The emphasis in the design should be placed on capturing as many different animals as

$t = 8$

CHAPTER 6 EXAMPLE 2

OCCASION	J=	1	2	3	4	5	6	7	8	
ANIMALS CAUGHT	N(J)=	19	26	33	27	33	37	27	28	
TOTAL CAUGHT	M(J)=	0	19	36	52	60	66	74	81	82
NEWLY CAUGHT	U(J)=	19	17	16	8	6	8	7	1	
FREQUENCIES	F(J)=	24	21	11	13	5	3	4	1	

$M_{t+1} = M_9 = 82$ = Total number of different animals captured

possible, possibly at the sacrifice of recaptures; that is, the probability of first capture p should be made as large as possible. One way to achieve this goal is to change the location of the traps between trapping occasions to increase the number of different areas of activity that are trapped effectively.

Example 3. Closure?

Perusal of the sample statistics given in Fig. 6.3a, created from another trapping experiment in the Florida sugar cane field, reveals a serious problem with respect to the assumption of closure. During the first 5 days of trapping, the number of newly caught animals steadily declines, as one would expect when trapping a population not subject to immigration. On the sixth day, however, the number of newly caught animals jumps to 20, and on the seventh and eight days as well, the numbers of unmarked animals caught are significant. This phenomenon should suggest an influx of new animals into the study area to the investigator, for it is not likely that such a severe jump in newly captured animals could occur without immigration. Unfortunately, the researcher cannot depend on the results of the closure test (Fig. 6.3b) to alert him to this possibility, because the test gives no indication that the closure assumption has been violated. This is not surprising, because the model selected as most appropriate for this data set is the behavioral response Model M_b (Fig. 6.3c), and as has been pointed out *(Otis et al. 1978:66)*, the closure test is not reliable in the presence of behavioral response. A warning signal exists, however, in the huge standard error of the population estimate, resulting in a coefficient of variation of 68%. In view of the suspected lack of closure, the researcher cannot present the estimate of 285 animals (Fig. 6.3d) as a valid estimate of the population size at the beginning of the experiment. Eliminating the last 3 days of trapping and reanalyzing the data probably would provide a better estimate of size at that time.

Example 4. Separating the Sexes

In Chapter 7, we point out that one potential method for eliminating individual heterogeneity in capture probabilities is to stratify the data into groups based on age, sex, or any other factor that the researcher may suspect as the cause of heterogeneity. The requirement that each subgroup have adequate data often prevents the use of this approach, but in a capture experiment in our Florida sugar cane field, ample data were collected and we were able to stratify them by sex. In this example, the objective was not so much to eliminate heterogeneity and thus improve the estimate of total population size as it was to satisfy a

Strong evidence of behavioral response

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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 =   38.216   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 =    9.892   DEGREES OF FREEDOM =   1   PROBABILITY OF LARGER VALUE =  0.00166


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 =   12.195   DEGREES OF FREEDOM =   7   PROBABILITY OF LARGER VALUE =  0.09434

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 =   12.828   DEGREES OF FREEDOM =   7   PROBABILITY OF LARGER VALUE =  0.07641

        TEST OF MODEL M(H) BY FREQUENCY OF CAPTURE
        (FREQUENCIES LESS THAN 2T ARE NOT CALCULATED.)

        NUMBER OF CAPTURES  CHI-SQUARE  D.F.  PROBABILITY
        ---------------------------------------------------

                1              14.000     7      0.05118
                2               7.444     7      0.38412


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 =   14.600   DEGREES OF FREEDOM =  12   PROBABILITY OF LARGER VALUE =  0.26404

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

        CHI-SQUARE VALUE =    5.795   DEGREES OF FREEDOM =   6   PROBABILITY OF LARGER VALUE =  0.44652

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

        CHI-SQUARE VALUE =    8.805   DEGREES OF FREEDOM =   6   PROBABILITY OF LARGER VALUE =  0.18485


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

        EXPECTED VALUES TOO SMALL.  TEST NOT PERFORMED.


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 =   32.358   DEGREES OF FREEDOM =  19   PROBABILITY OF LARGER VALUE =  0.02847

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   0.74     0.77     1.00     0.93     0.00     0.37     0.76     0.79


APPROPRIATE MODEL PROBABLY IS M(B)
SUGGESTED ESTIMATOR IS ZIPPIN.
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Evidence of trap response even in the presence of individual heterogeneity

Fig. 6.2b. Output from the model selection procedure.

Probability of capture increases after first capture - animals are evidently trap happy

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CHAPTER 6 EXAMPLE 2

OCCASION            J=      1    2    3    4    5    6    7    8
TOTAL CAUGHT     M(J)=      0   19   36   52   60   66   74   81   82
NEWLY CAUGHT     U(J)=     19   17   16    8    6    8    7    1

ESTIMATED PROBABILITY OF CAPTURE, P-HAT =   0.230132

ESTIMATED PROBABILITY OF RECAPTURE, C-HAT = 0.381443


POPULATION ESTIMATE IS           93 WITH STANDARD ERROR      6.6865

APPROXIMATE 95 PERCENT CONFIDENCE INTERVALS          79 TO         107


HISTOGRAM OF U(J)


FREQUENCY      19   17   16    8    6    8    7    1
-----------------------------------------------------
EACH * EQUALS     2 POINTS

      20        *
      18        *    *
      16        *    *    *
      14        *    *    *
      12        *    *    *
      10        *    *    *
       8        *    *    *    *         *    *
       6        *    *    *    *    *    *    *
       4        *    *    *    *    *    *    *
       2        *    *    *    *    *    *    *    *
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Fig. 6.2c. Estimates of population size and capture probabilities produced by the Zippin procedure for the original data.

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CHAPTER 6 EXAMPLE 2 - MANIPULATED

OCCASION             J=     1    2    3    4    5    6    7    8
ANIMALS CAUGHT    N(J)=    19   17   18   12   11   13   12    8
TOTAL CAUGHT      M(J)=     0   19   36   52   60   66   74   81   82
NEWLY CAUGHT      U(J)=    19   17   16    8    6    8    7    1
FREQUENCIES       F(J)=    67    7    3    5    0    0    0    0
```

The sequence of first captures is the same as before, but total daily captures have decreased because animals have been made trap shy

Fig. 6.2d. The summary statistics for the manipulated trap-shy data set.

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CHAPTER 6 EXAMPLE 2 - MANIPULATED

OCCASION           J=     1    2    3    4    5    6    7    8
TOTAL CAUGHT    M(J)=     0   19   36   52   60   66   74   81   82
NEWLY CAUGHT    U(J)=    19   17   16    8    6    8    7    1

ESTIMATED PROBABILITY OF CAPTURE, P-HAT =   0.230132

ESTIMATED PROBABILITY OF RECAPTURE, C-HAT = 0.072165


POPULATION ESTIMATE IS          93 WITH STANDARD ERROR     6.6865

APPROXIMATE 95 PERCENT CONFIDENCE INTERVALS          79 TO          107


HISTOGRAM OF U(J)


FREQUENCY      19   17   16    8    6    8    7    1
------------------------------------------------------
EACH * EQUALS     2 POINTS

      20       *
      18       *    *
      16       *    *    *
      14       *    *    *
      12            *    *
      10                 *
       8                 *    *         *    *
       6       *    *    *    *    *    *    *
       4       *    *    *    *    *    *    *
       2       *    *    *    *    *    *    *    *
------------------------------------------------------
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Estimates of p and N have remained the same, even though the probability of recapture has fallen from 0.38 to 0.07!

Fig. 6.2e. Estimates of population size and capture probabilities for the manipulated data set.

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CHAPTER 6 EXAMPLE 3

OCCASION            J=     1    2    3    4    5    6    7    8
ANIMALS CAUGHT   N(J)=    17   16   16   17   12   29   29   25
TOTAL CAUGHT     M(J)=     0   17   30   41   51   58   78   91   98
NEWLY CAUGHT     U(J)=    17   13   11   10    7   20   13    7
FREQUENCIES      F(J)=    55   31    7    3    1    1    0    0
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Evidence of immigration

The closure test fails to detect evidence of the apparent breakdown of closure

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CHAPTER 6 EXAMPLE 3

          OVERALL TEST RESULTS --
          Z-VALUE                                  0.824
          PROBABILITY OF A SMALLER VALUE         0.79498

          TEST OF CLOSURE BY FREQUENCY OF CAPTURE.
          (FREQUENCIES LESS THAN 10 ARE NOT COMPUTED.)

          NUMBER OF CAPTURES   Z-VALUE   PROBABILITY
          ----------------------------------------
                  2             -.207      0.41785
```

See Figure 2.9 in Chapter 2

Fig. 6.3b. The formal test for population closure.

curiosity about (1) the relative sizes of populations by sex, (2) the relative catchability of the sexes, and (3) whether individual differences in catchability could be ascribed to sex. Figure 6.4a shows a summary of the entire data set, and Fig. 6.4b reveals that analysis of the data results in an excellent fit to the heterogeneity Model M_h. The population estimate of 391 (S.E. = 36) is entirely satisfactory in terms of standard error (Fig. 6.4c). The analyses for males and females are given in Figs. 6.4d-f and 6.4g-i, respectively. With respect to the males, we notice that Models M_o and M_h both receive values of 1.00 in the model selection procedure, and that the Model M_h is chosen for the estimation. This choice has been built into program CAPTURE because Model M_h has the more robust estimator; that is, we believe that it is the "safer" model to use when the selection process produces a tie. The estimate of the male population size is 211 (S.E. = 21), and the estimate of average capture probability of males is 0.1013, a figure that is very close to the corresponding estimate of 0.1087 for the entire population. Similar results are produced for females. Model M_h is chosen and proves to be a much more solid choice than it was for males. The estimate of female population size is 148 (S.E. = 15), and the estimate of 0.1427 for the average probability of capture is again close to the corresponding figure for the entire population.

Have the analyses satisfied our earlier curiosities? First, we should test to see if the population estimates for each sex are different. A simple method is the z-test, which assumes that the estimates of N are distributed normally, with known variance. These conditions should hold at least approximately when sample size is large. We assume that our sample meets these assumptions. The null hypothesis is $H_0 : N_♂ = N_♀$. The two-tailed z-test is calculated as

$$z = \frac{\hat{N}_♂ - \hat{N}_♀}{\sqrt{\hat{V}ar(\hat{N}_♂) + \hat{V}ar(\hat{N}_♀)}} \, .$$

CHAPTER 6 EXAMPLE 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 = 8.808 DEGREES OF FREEDOM = 3 PROBABILITY OF LARGER VALUE = 0.03196

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

CHI-SQUARE VALUE = 6.769 DEGREES OF FREEDOM = 1 PROBABILITY OF LARGER VALUE = 0.00928

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 = 16.849 DEGREES OF FREEDOM = 7 PROBABILITY OF LARGER VALUE = 0.01840

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 = 17.982 DEGREES OF FREEDOM = 7 PROBABILITY OF LARGER VALUE = 0.01205

TEST OF MODEL M(H) BY FREQUENCY OF CAPTURE
(FREQUENCIES LESS THAN 2T ARE NOT CALCULATED.)

NUMBER OF CAPTURES	CHI-SQUARE	D.F.	PROBABILITY
1	11.473	7	0.11929
2	11.366	7	0.12345

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 = 14.705 DEGREES OF FREEDOM = 12 PROBABILITY OF LARGER VALUE = 0.25796

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

CHI-SQUARE VALUE = 11.598 DEGREES OF FREEDOM = 6 PROBABILITY OF LARGER VALUE = 0.07157

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

CHI-SQUARE VALUE = 3.108 DEGREES OF FREEDOM = 6 PROBABILITY OF LARGER VALUE = 0.79522

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

EXPECTED VALUES TOO SMALL. TEST NOT PERFORMED.

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 = 35.797 DEGREES OF FREEDOM = 14 PROBABILITY OF LARGER VALUE = 0.00112

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	0.48	0.41	1.00	0.70	0.00	0.27	0.73	0.48

APPROPRIATE MODEL PROBABLY IS M(B)
SUGGESTED ESTIMATOR IS ZIPPIN.

Model M_b gives a good fit to the data; therefore it is not suprising that it is chosen as the best model

Fig. 6.3c. The results of tests of capture probability structure and the model selection procedure.

Width of the confidence interval reflects the total unreliability of the population estimate. This is the best evidence the biologist has of the fact that lack of closure has prevented production of a good estimate

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CHAPTER 6 EXAMPLE 3

OCCASION            J=    1    2    3    4    5    6    7    8
TOTAL CAUGHT     M(J)=    0   17   30   41   51   58   78   91   98
NEWLY CAUGHT     U(J)=   17   13   11   10    7   20   13    7

ESTIMATED PROBABILITY OF CAPTURE, P-HAT =   0.051280

ESTIMATED PROBABILITY OF RECAPTURE, C-HAT = 0.172131


POPULATION ESTIMATE IS         285 WITH STANDARD ERROR   194.1353

APPROXIMATE 95 PERCENT CONFIDENCE INTERVALS        -95 TO        666


HISTOGRAM OF U(J)


FREQUENCY       17   13   11   10    7   20   13    7
-------------------------------------------------------
EACH * EQUALS    2 POINTS

       20                                 *
       18        *                        *
       16        *                        *
       14        *    *                   *    *
       12        *    *    *              *    *
       10        *    *    *    *         *    *
        8        *    *    *    *    *    *    *    *
        6        *    *    *    *    *    *    *    *
        4        *    *    *    *    *    *    *    *
        2        *    *    *    *    *    *    *    *
-------------------------------------------------------
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Visual representation of the apparent influx of new animals

Fig. 6.3d. Population estimation using Model M_b.

CHAPTER 6 EXAMPLE 4 - SEXES COMBINED

OCCASION	J=	1	2	3	4	5	6	7	8	
ANIMALS CAUGHT	N(J)=	44	38	44	47	45	44	45	33	
TOTAL CAUGHT	M(J)=	0	44	74	102	129	152	172	185	194
NEWLY CAUGHT	U(J)=	44	30	28	27	23	20	13	9	
FREQUENCIES	F(J)=	109	47	26	5	3	4	0	0	

A total of 109 animals were captured only once, and 47 animals were captured exactly twice

Fig. 6.4a. An example of stratification of the trapping data by sex, using results of an experiment on the cotton rat. The summary statistics are for the entire data set.

Substituting the numbers from Figs. 6.4f and 6.4i gives

$$z = \frac{211 - 148}{\sqrt{20.87^2 + 15.21^2}}$$

$$= 2.44 \ .$$

The probability of a larger z value (taken from a z or standard normal deviate table) is 0.0146. We thus conclude that the populations of the two sexes differ in size and, because $\hat{N}_{♂} > \hat{N}_{♀}$, that there are more males than females.

The same approach could be used to test for differences in average capture probability between the sexes, but the procedure is not straightforward because of the difficulty in estimating the variances of these estimates. Even without such a test at our disposal, we can say that no biologically significant differences exist between the two parameters; the estimates are 0.10 for males and 0.14 for females. Furthermore, we can say that sex is not the cause of heterogeneous capture probabilities in the population.

Thus, we have seen that the population size appears to be weighted in favor of males and that, on the basis of subjective evaluation, the average male is about as catchable as the average female. Furthermore, we must conclude that individual heterogeneity in capture probabilities is present within each sex, although we find indications that such differences may not be quite as large among males. Finally, we point out that the estimates from the two sexes add up to 359 animals, a figure that is close to the estimate of 391 produced from the entire data set. In general, the estimate obtained by summing the individual subgroup estimates will not equal the estimate produced from the entire data set; in fact, the two can be quite different, particularly if different models are selected in the analyses. In this instance, however, close agreement between the two estimates is reached, probably because of the consistent use of the jackknife estimator and the similarity in capture probabilities between the two sexes.

Example 5. Time Is of the Essence

We have described eight different probability models for capture-recapture experiments and discovered that three of them (M_{tb}, M_{th}, and M_{tbh}) do not have associated estimators. In each of these models, only the time factor appears consistently, and all the corresponding models without this factor (M_b, M_h, and M_{bh}) have associated estimators. Thus, if time is not a factor affecting capture probabilities, the

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CHAPTER 6 EXAMPLE 4 - SEXES COMBINED

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 =   35.250   DEGREES OF FREEDOM =   3   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 =    0.000   DEGREES OF FREEDOM =   1   PROBABILITY OF LARGER VALUE =  0.99596


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 =    4.798   DEGREES OF FREEDOM =   7   PROBABILITY OF LARGER VALUE =  0.68463

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 =    4.444   DEGREES OF FREEDOM =   7   PROBABILITY OF LARGER VALUE =  0.72740

        TEST OF MODEL M(H) BY FREQUENCY OF CAPTURE
        (FREQUENCIES LESS THAN 2T ARE NOT CALCULATED.)

        NUMBER OF CAPTURES  CHI-SQUARE  D.F.  PROBABILITY
        -----------------------------------------------

                1                7.330     7      0.39532
                2                7.099     7      0.41862
                3                1.651     7      0.97661


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 =    7.095   DEGREES OF FREEDOM =  12   PROBABILITY OF LARGER VALUE =  0.85129

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

        CHI-SQUARE VALUE =    2.844   DEGREES OF FREEDOM =   6   PROBABILITY OF LARGER VALUE =  0.82810

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

        CHI-SQUARE VALUE =    4.250   DEGREES OF FREEDOM =   6   PROBABILITY OF LARGER VALUE =  0.64286

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 =  204.825   DEGREES OF FREEDOM = 147   PROBABILITY OF LARGER VALUE =  0.00090


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 =   23.447   DEGREES OF FREEDOM =  19   PROBABILITY OF LARGER VALUE =  0.21822

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   0.63      1.00      0.15      0.37      0.00      0.24      0.22      0.41


APPROPRIATE MODEL PROBABLY IS M(H)
SUGGESTED ESTIMATOR IS JACKKNIFE.
```

Model M_t is a very poor model for these data

Fig. 6.4b. The results of the model selection procedure, using data from both sexes.

```
CHAPTER 6 EXAMPLE 4 - SEXES COMBINED

NUMBER OF TRAPPING OCCASIONS WAS              8
NUMBER OF ANIMALS CAPTURED, M(T+1), WAS     194
TOTAL NUMBER OF CAPTURES, N., WAS           340

FREQUENCIES OF CAPTURE,F(I)
   I=   1  2  3  4  5 6 7 8
F(I)= 109 47 26  5  3 4 0 0

          COMPUTED JACKKNIFE COEFFICIENTS

          N(1)      N(2)      N(3)      N(4)      N(5)
    1  1.875     2.625     3.250     3.750     4.125
    2  1.000     0.357     -.625    -1.696    -2.661
    3  1.000     1.000     1.372     2.098     2.964
    4  1.000     1.000     1.000     0.848     0.535
    5  1.000     1.000     1.000     1.000     1.036

          THE RESULTS OF THE JACKKNIFE COMPUTATIONS

  I       N(I)   SE(I)   0.95 CONF. LIMITS     TEST OF N(I+1) VS. N(I)
  0      194                                   CHI-SQUARE(1 D.F.)
  1      289.4    13.37    263.2    315.6          39.410
  2      340.9    21.31    299.1    382.7          11.531
  3      372.5    29.29    315.1    430.0           5.331
  4      394.8    37.39    321.5    468.1           3.540
  5      411.4    44.87    323.5    499.4           0.000

AVERAGE P-HAT = 0.1087

INTERPOLATED POPULATION ESTIMATE IS      391 WITH STANDARD ERROR    35.9808

APPROXIMATE 95 PERCENT CONFIDENCE INTERVAL        320 TO        462


HISTOGRAM OF F(I)

FREQUENCY     109  47  26   5   3   4   0   0
-------------------------------------------------------
EACH * EQUALS    11 POINTS

     110       *
      99       *
      88       *
      77       *
      66       *
      55       *
      44       *   *
      33       *   *
      22       *   *   *
      11       *   *   *
-------------------------------------------------------
```

Average catchability of the population is estimated to be 0.11 - fairly low

Fig. 6.4c. Population estimation of the total population, using the Model M_h procedure.

```
CHAPTER 6 EXAMPLE 4 - MALES

OCCASION            J=    1   2   3   4   5   6   7   8
ANIMALS CAUGHT   N(J)=   18  17  18  28  24  25  26  15
TOTAL CAUGHT     M(J)=    0  18  33  46  67  82  93 102 108
NEWLY CAUGHT     U(J)=   18  15  13  21  15  11   9   6
FREQUENCIES      F(J)=   66  27  11   3   0   1   0   0
```

Fig. 6.4d. The summary statistics for the males.

There were 5 (=18-13) recaptures on the third trapping occasion

CHAPTER 6 EXAMPLE 4 - MALES

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 = 3.844 DEGREES OF FREEDOM = 3 PROBABILITY OF LARGER VALUE = 0.27886

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

CHI-SQUARE VALUE = 0.511 DEGREES OF FREEDOM = 1 PROBABILITY OF LARGER VALUE = 0.47478

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 = 9.256 DEGREES OF FREEDOM = 7 PROBABILITY OF LARGER VALUE = 0.23480

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 = 9.299 DEGREES OF FREEDOM = 7 PROBABILITY OF LARGER VALUE = 0.23192

TEST OF MODEL M(H) BY FREQUENCY OF CAPTURE
(FREQUENCIES LESS THAN 2T ARE NOT CALCULATED.)

NUMBER OF CAPTURES	CHI-SQUARE	D.F.	PROBABILITY
1	6.970	7	0.43204
2	11.321	7	0.12522

No evidence of significant variation among daily captures

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 = 10.600 DEGREES OF FREEDOM = 12 PROBABILITY OF LARGER VALUE = 0.56346

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

CHI-SQUARE VALUE = 6.142 DEGREES OF FREEDOM = 6 PROBABILITY OF LARGER VALUE = 0.40743

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

CHI-SQUARE VALUE = 4.458 DEGREES OF FREEDOM = 6 PROBABILITY OF LARGER VALUE = 0.61497

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 = 26.084 DEGREES OF FREEDOM = 20 PROBABILITY OF LARGER VALUE = 0.16305

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 = 12.078 DEGREES OF FREEDOM = 14 PROBABILITY OF LARGER VALUE = 0.60001

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	1.00	1.00	0.37	0.60	0.00	0.53	0.41	0.72

APPROPRIATE MODEL PROBABLY IS M(H) OR M(O)
SUGGESTED ESTIMATOR IS JACKKNIFE.

These two models have tied for best model - The jackknife (Model M_h) estimator is chosen because it is a more robust (see Chapter 2) estimator

Fig. 6.4e. The results of the model selection procedure for males.

A total of 108 males were captured during the experiment

```
CHAPTER 6 EXAMPLE 4 - MALES

NUMBER OF TRAPPING OCCASIONS WAS                  8
NUMBER OF ANIMALS CAPTURED, M(T+1), WAS         108
TOTAL NUMBER OF CAPTURES, N., WAS               171

FREQUENCIES OF CAPTURE,F(I)
   I=   1   2   3   4   5  6  7  8
F(I)=  66  27  11   3   0  1  0  0

         COMPUTED JACKKNIFE COEFFICIENTS

          N(1)       N(2)       N(3)       N(4)       N(5)
     1  1.875      2.625      3.250      3.750      4.125
     2  1.000      0.357      -.625     -1.696     -2.661
     3  1.000      1.000      1.372      2.098      2.964
     4  1.000      1.000      1.000      0.848      0.535
     5  1.000      1.000      1.000      1.000      1.036

         THE RESULTS OF THE JACKKNIFE COMPUTATIONS

 I        N(I)    SE(I)    0.95 CONF. LIMITS       TEST OF N(I+1) VS. N(I)
 0      108                                           CHI-SQUARE(1 D.F.)
 1      165.8     10.41      145.4      186.1          26.438
 2      197.9     16.59      165.4      230.4           7.012
 3      216.7     22.71      172.2      261.2           2.559
 4      228.3     28.79      171.9      284.8           1.245
 5      235.6     34.31      168.4      302.9           0.000

AVERAGE P-HAT = 0.1013

INTERPOLATED POPULATION ESTIMATE IS        211 WITH STANDARD ERROR    20.8709

APPROXIMATE 95 PERCENT CONFIDENCE INTERVAL        170 TO       253


HISTOGRAM OF F(I)

FREQUENCY       66   27   11    3    0    1    0    0
-----------------------------------------------------
EACH * EQUALS     7 POINTS

       63        *
       56        *
       49        *
       42        *
       35        *
       28        *    *
       21        *    *
       14        *    *    *
        7        *    *    *
-----------------------------------------------------
```

Fig. 6.4f. Population estimation of the male population, using the Model M_h procedure.

```
CHAPTER 6 EXAMPLE 4 - FEMALES

OCCASION          J=     1    2    3    4    5    6    7    8
ANIMALS CAUGHT  N(J)=   26   21   26   19   21   19   19   18
TOTAL CAUGHT    M(J)=    0   26   41   56   62   70   79   83   86
NEWLY CAUGHT    U(J)=   26   15   15    6    8    9    4    3
FREQUENCIES     F(J)=   43   20   15    2    3    3    0    0
```

Fig. 6.4g. The summary statistics for the females.

```
CHAPTER 6 EXAMPLE 4 - FEMALES

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 =   26.293   DEGREES OF FREEDOM =   3   PROBABILITY OF LARGER VALUE =  0.00001


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

        CHI-SQUARE VALUE =    1.360   DEGREES OF FREEDOM =   1   PROBABILITY OF LARGER VALUE =  0.24354


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 =    3.966   DEGREES OF FREEDOM =   7   PROBABILITY OF LARGER VALUE =  0.78365

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 =    4.515   DEGREES OF FREEDOM =   7   PROBABILITY OF LARGER VALUE =  0.71887

        TEST OF MODEL M(H) BY FREQUENCY OF CAPTURE
        (FREQUENCIES LESS THAN 2T ARE NOT CALCULATED.)

        NUMBER OF CAPTURES  CHI-SQUARE  D.F.  PROBABILITY
        -------------------------------------------------

                1                8.535     7     0.28780
                2                3.733     7     0.80993


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 =    7.977   DEGREES OF FREEDOM =  12   PROBABILITY OF LARGER VALUE =  0.78693

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

        CHI-SQUARE VALUE =    4.548   DEGREES OF FREEDOM =   6   PROBABILITY OF LARGER VALUE =  0.60292

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

        CHI-SQUARE VALUE =    3.429   DEGREES OF FREEDOM =   6   PROBABILITY OF LARGER VALUE =  0.75342


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 =   47.103   DEGREES OF FREEDOM =  25   PROBABILITY OF LARGER VALUE =  0.00477


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 =   14.969   DEGREES OF FREEDOM =  16   PROBABILITY OF LARGER VALUE =  0.52689

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    0.58       1.00       0.20       0.48       0.00       0.25       0.20       0.50


APPROPRIATE MODEL PROBABLY IS M(H)
SUGGESTED ESTIMATOR IS JACKKNIFE.
```

Fig. 6.4h. The results of the model selection procedure for females.

No females were
captured every day

```
CHAPTER 6 EXAMPLE 4 - FEMALES

NUMBER OF TRAPPING OCCASIONS WAS               8
NUMBER OF ANIMALS CAPTURED, M(T+1), WAS       86
TOTAL NUMBER OF CAPTURES, N., WAS            169

FREQUENCIES OF CAPTURE,F(I)
   I=   1   2   3   4   5   6   7   8
F(I)=  43  20  15   2   3   3   0   0

         COMPUTED JACKKNIFE COEFFICIENTS

          N(1)       N(2)       N(3)       N(4)       N(5)
    1   1.875      2.625      3.250      3.750      4.125
    2   1.000      0.357      -.625     -1.696     -2.661
    3   1.000      1.000      1.372      2.098      2.964
    4   1.000      1.000      1.000      0.848      0.535
    5   1.000      1.000      1.000      1.000      1.036

         THE RESULTS OF THE JACKKNIFE COMPUTATIONS

 I       N(I)    SE(I)    0.95 CONF. LIMITS      TEST OF N(I+1) VS. N(I)
 0        86                                        CHI-SQUARE(1 D.F.)
 1      123.6     8.40     107.2      140.1          13.238
 2      143.0    13.37     116.8      169.2           4.475
 3      155.8    18.50     119.6      192.1           2.784
 4      166.5    23.86     119.7      213.3           2.444
 5      175.8    28.91     119.1      232.5           0.000

AVERAGE P-HAT = 0.1427

INTERPOLATED POPULATION ESTIMATE IS         148 WITH STANDARD ERROR     15.2086

APPROXIMATE 95 PERCENT CONFIDENCE INTERVAL        118 TO        178


HISTOGRAM OF F(I)

FREQUENCY      43   20   15    2    3    3    0    0
-------------------------------------------------------
EACH * EQUALS     5 POINTS

      45        *
      40        *
      35        *
      30        *
      25        *
      20        *    *
      15        *    *    *
      10        *    *    *
       5        *    *    *         *    *
-------------------------------------------------------
```

A coefficient of variation
of ≈ 10 % - not bad!

Fig. 6.4i. Population estimation of the female population, using the Model M_h procedure.

researcher is assured that the most appropriate model selected for the data will produce an estimate. This fact has important implications for study design. Clearly, the experimentor should do everything possible to avoid the situation in which one of these "no estimator" models is most appropriate for the experiment.

Usually we think of weather changes as the cause of differential trap success among trapping occasions, or significant time variation. The reader may ask whether we are suggesting that uniform weather conditions be designed into the experiment. The answer is no. We realize that such designs are difficult to come by. However, another parameter of the experiment is controllable and also is a potential cause of time variation. This parameter is effort; it can be measured both in terms of the number of traps used and the frequency with which they are checked. Thus, to help achieve uniform trapping success, the same number of traps should be used on each trapping occasion (usually a day), and the traps should be checked the same number of times each day. To illustrate this point, let us consider the results of an experiment on Richardson's ground squirrels *(Spermophilus richardsoni)* in an abandoned wheat field in the rangeland of southwestern Montana.

In the experiment, 93 livetraps were placed by active burrow holes in the 1.5-ha (3.8-acre) study plot, baited with rolled oats, and checked for 6 consecutive days. Although the entire group of traps was checked more than once daily, the trapping occasion was defined as 1 day, and therefore the captures resulting from separate trap checks within the day were pooled.

On the first day of trapping, traps were checked twice, but on each of the remaining days, they were checked three times. The reason for this is simple—on the first day, there was not time to check the traps three times because trapping success was high and every animal had to be handled and tagged. On subsequent days, recaptures (which demand less time than new captures) increased, and the researchers became more efficient. In the summary statistics for the trapping experiment (Fig. 6.5a) the daily captures reflect almost perfectly the effect of unequal trapping effort. The number caught on the first day is only about two-thirds of the numbers caught on each remaining day. Thus, as the model selection procedure (Fig. 6.5b) indicates, significant time variation is included in the selected Model M_{tbh}. However, Figs. 6.5c-e reveal the excellent results produced when we use only the data from the last 5 days of trapping, when effort was equal. The lesson here is plain: devote equal effort to each trapping occasion or risk the chance that trapping effort on some occasions may be wasted. Equal effort on each trapping occasion is a fundamental assumption of all eight models described in Chapter 3.

Example 6. How Many Are Not Enough?

We frequently emphasize that we do not recommend using capture-recapture estimation procedures when the population to be trapped is expected to be "small." The researcher often responds by asking, "Why not, when I have used capture-recapture before in such situations and obtained reasonable-looking population estimates with small standard errors?" Such a question is to be expected, because of data sets like the one presented in Fig. 6.6a. The data were collected from a study site in Idaho, which had been clearcut in the 1960s and recently replanted with lodgepole pine *(Pinus contorta)* seedlings. A 10 by 10

CHAPTER 6 EXAMPLE 5 - ALL OCCASIONS

OCCASION	J=	1	2	3	4	5	6	
ANIMALS CAUGHT	N(J)=	127	193	180	176	173	193	
TOTAL CAUGHT	M(J)=	0	127	254	319	356	385	406
NEWLY CAUGHT	U(J)=	127	127	65	37	29	21	
FREQUENCIES	F(J)=	121	102	74	68	23	18	

Fig. 6.5a. The summary statistics for an experiment on Richardson's ground squirrels, illustrating the importance of equal effort on all trapping occasions.

On Day 2, 66 more animals
were captured than on Day 1

CHAPTER 6 EXAMPLE 5 - ALL OCCASIONS

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 = 181.481 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 = 19.438 DEGREES OF FREEDOM = 1 PROBABILITY OF LARGER VALUE = 0.00001

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 = 31.975 DEGREES OF FREEDOM = 5 PROBABILITY OF LARGER VALUE = 0.00001

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 = 32.462 DEGREES OF FREEDOM = 5 PROBABILITY OF LARGER VALUE = 0.00001

TEST OF MODEL M(H) BY FREQUENCY OF CAPTURE
(FREQUENCIES LESS THAN 2T ARE NOT CALCULATED.)

NUMBER OF CAPTURES	CHI-SQUARE	D.F.	PROBABILITY
1	6.587	5	0.25323
2	6.912	5	0.22729
3	20.450	5	0.00103
4	13.199	5	0.02159
5	9.087	5	0.10565

Strong evidence of time variation

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 = 17.554 DEGREES OF FREEDOM = 8 PROBABILITY OF LARGER VALUE = 0.02483

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

CHI-SQUARE VALUE = 12.212 DEGREES OF FREEDOM = 4 PROBABILITY OF LARGER VALUE = 0.01585

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

CHI-SQUARE VALUE = 5.342 DEGREES OF FREEDOM = 4 PROBABILITY OF LARGER VALUE = 0.25394

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 = 519.588 DEGREES OF FREEDOM = 316 PROBABILITY OF LARGER VALUE = 0.00000

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 = 39.514 DEGREES OF FREEDOM = 15 PROBABILITY OF LARGER VALUE = 0.00054

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	0.57	0.49	0.46	0.87	0.00	0.46	0.49	1.00

APPROPRIATE MODEL PROBABLY IS M(TBH)
NO ESTIMATOR RESULTS FROM THIS MODEL.

Selection of Model M_{TBH} is to be expected because all null hypotheses tested above (with the exception of Test 5b) were rejected

Fig. 6.5b. Output from the model selection procedure.

CHAPTER 6 EXAMPLE 5 - OCCASION 1 ELIMINATED

OCCASION	J=	1	2	3	4	5	
ANIMALS CAUGHT	N(J)=	193	180	176	173	193	
TOTAL CAUGHT	M(J)=	0	193	294	336	367	393
NEWLY CAUGHT	U(J)=	193	101	42	31	26	
FREQUENCIES	F(J)=	132	102	82	52	25	

Fig. 6.5c. The summary statistics for the data from only the last 5 days of trapping.

grid of 100 livetraps spaced at 15-m intervals was used to trap the area for 5 consecutive days, to estimate the size of the small mammal population. The traps, baited with a mixture of rolled oats and peanut butter, were checked in the morning and evening. (The data in Fig. 6.6a have been pooled to obtain daily captures.)

The results of the model selection and estimation tasks are given in Figs. 6.6b and 6.6c. Only Test 7 indicates variation in capture probabilities, and samples are too small to compute two of the tests. Thus, the choice of M_o, the simplest model, as most appropriate is not surprising. Although the estimated population size is the same as the number of animals captured, this estimate seems reasonable and appears to be very precise.

Why then do we recommend that results obtained from experiments in which very few animals are captured not be trusted? Let us view the results of this example in light of a small simulation study that was conducted to evaluate model selection and estimation procedures when the population is small and trapping success moderate. The study generated 100 sets of data from each of the 8 models. Population size was 50, the average probability of capture was about 0.20 in each model, and trapping was done on 6 occasions.

The following relevant conclusions arose from the study.

1. The procedures performed satisfactorily when the data were generated from Model M_o or Model M_t.
2. Model M_o was chosen as the most appropriate model in nearly 75% of the data sets generated from Models M_b, M_h, M_{bh}, and M_{th}. In these instances, the estimate averaged 42.5, and the confidence interval coverage was about 50%. The correct model was selected only about 8% of the time.
3. The correct model was selected in 62 of the 100 data sets generated from M_{tb}; M_o was selected only 3 times, and these 3 estimates averaged 72.3.
4. The correct model was selected in only 1 of the 100 data sets generated from M_{tbh}; M_o was selected 4 times, and these estimates averaged 59.5.

How do these results affect our interpretation of the real world example? The second point above has particular relevance for us; it says that the chances are very good that Model M_o is not a good model for the data, that the estimate therefore is biased, and that the presumed 95% confidence interval is probably closer to a 50% confidence interval.

Taken as a whole, this example illustrates one central point: unless both behavioral response and heterogeneity are absent, the model selection and estimation procedures are likely to produce misleading results when small populations are involved. The answer will be precise, with a small confidence interval, but misleading.

Example 7. Density Estimation

The method described in Chapter 5 for estimating density is again illustrated here, by a data set collected from a population of Richardson's ground squirrels. Trapping was done on a 10 by 10 grid with one trap per station and a 10-m trap spacing, for five trapping occasions. The number of animals captured per station and the definition of the four subgrids to be used to estimate density are given in Fig. 6.7a.

The results of three tests of a null hypothesis concerning uniform density over the grid are given in Fig. 6.7b. Although there is no evidence of a gradient in the direction of columns or with respect to distance

Time specific variation has been eliminated by excluding the first day of trapping

```
CHAPTER 6 EXAMPLE 5 - OCCASION 1 ELIMINATED

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 =   87.624   DEGREES OF FREEDOM =   3   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 =    0.078   DEGREES OF FREEDOM =   1   PROBABILITY OF LARGER VALUE =  0.78022

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 =    3.499   DEGREES OF FREEDOM =   4   PROBABILITY OF LARGER VALUE =  0.47806

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 =    3.891   DEGREES OF FREEDOM =   4   PROBABILITY OF LARGER VALUE =  0.42092

        TEST OF MODEL M(H) BY FREQUENCY OF CAPTURE
        (FREQUENCIES LESS THAN 2T ARE NOT CALCULATED.)

        NUMBER OF CAPTURES  CHI-SQUARE  D.F.  PROBABILITY
        ---------------------------------------------------

              1                4.061     4     0.39787
              2                1.203     4     0.87767
              3                6.455     4     0.16763
              4               15.308     4     0.00410
```

The data are now fit nicely by Model M_h

```
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 =   10.248   DEGREES OF FREEDOM =   6   PROBABILITY OF LARGER VALUE =  0.11458

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

        CHI-SQUARE VALUE =    8.473   DEGREES OF FREEDOM =   3   PROBABILITY OF LARGER VALUE =  0.03719

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

        CHI-SQUARE VALUE =    1.776   DEGREES OF FREEDOM =   3   PROBABILITY OF LARGER VALUE =  0.62028

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 =  455.905   DEGREES OF FREEDOM = 292   PROBABILITY OF LARGER VALUE =  0.00000

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 =   11.025   DEGREES OF FREEDOM =  10   PROBABILITY OF LARGER VALUE =  0.35554

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   0.69    1.00    0.29    0.41    0.00    0.34    0.24    0.56

APPROPRIATE MODEL PROBABLY IS M(H)
SUGGESTED ESTIMATOR IS JACKKNIFE.
```

Model M_t continues to be a poor model for these data

Fig. 6.5d. Output from the model selection procedure when Day 1 is eliminated.

```
CHAPTER 6 EXAMPLE 5 - OCCASION 1 ELIMINATED

NUMBER OF TRAPPING OCCASIONS WAS                    5
NUMBER OF ANIMALS CAPTURED, M(T+1), WAS           393
TOTAL NUMBER OF CAPTURES, N., WAS                 915

FREQUENCIES OF CAPTURE,F(I)
   I=   1   2   3   4   5
F(I)= 132 102  82  52  25

         COMPUTED JACKKNIFE COEFFICIENTS

         N(1)       N(2)       N(3)       N(4)       N(5)
    1   1.600      2.400      2.800      3.000      3.000
    2   1.000      0.550      0.050      -.250      -.250
    3   1.000      1.000      1.133      1.250      1.250
    4   1.000      1.000      1.000      0.992      0.992
    5   1.000      1.000      1.000      1.000      1.000


         THE RESULTS OF THE JACKKNIFE COMPUTATIONS

 I       N(I)    SE(I)    0.95 CONF. LIMITS       TEST OF N(I+1) VS. N(I)
 0      393                                          CHI-SQUARE(1 D.F.)
 1      498.6     13.79     471.6     525.6            16.924
 2      531.9     20.45     491.8     572.0             3.393
 3      544.6     25.94     493.8     595.5             1.564
 4      549.6     29.14     492.5     606.7             0.000
 5      549.6     29.14     492.5     606.7             0.000

AVERAGE P-HAT = 0.3446

INTERPOLATED POPULATION ESTIMATE IS          531 WITH STANDARD ERROR    20.2128

APPROXIMATE 95 PERCENT CONFIDENCE INTERVAL        491 TO         571


HISTOGRAM OF F(I)

FREQUENCY      132  102   82   52   25
----------------------------------------
EACH * EQUALS     14 POINTS

      126        *
      112        *
       98        *    *
       84        *    *    *
       70        *    *    *
       56        *    *    *    *
       42        *    *    *    *
       28        *    *    *    *    *
       14        *    *    *    *    *
----------------------------------------
```

High average probability of capture, and a corresponding small standard error are two qualities the experimentor should strive for

Fig. 6.5e. Estimation of population size, using the jacknife estimator (Model M_h) on data from Days 2-6.

CHAPTER 6 EXAMPLE 6

OCCASION	J=	1	2	3	4	5	
ANIMALS CAUGHT	N(J)=	13	16	17	18	15	
TOTAL CAUGHT	M(J)=	0	13	20	23	24	24
NEWLY CAUGHT	U(J)=	13	7	3	1	0	
FREQUENCIES	F(J)=	4	3	4	8	5	

Only 24 different animals were captured in 5 days of trapping

Fig. 6.6a. The summary statistics illustrating a trapping experiment on small mammals in which few animals were captured.

from the center of the grid, there is evidence ($P < 0.05$) that density is greater on the bottom half of the grid. In this instance, however, the estimation procedure should not be biased with respect to estimating average density on the grid, because of the configuration of the nested subgrids. The area of every subgrid is divided evenly between the "high" and "low" density areas. This advantage of the nested design also should hold if the density pattern in the direction of columns is similar.

Estimates of population size on each of the subgrids are presented in Figs. 6.7c-6.7f. Previous analysis of the entire data set, using the model selection procedure, indicated that the Model M_{bh} estimator provided the most reliable estimates, and therefore this estimator was chosen for use on all subgrids. In general, adequate fits to the data were obtained for all four data sets.

Figure 6.7g first gives the starting values for parameters essential to the actual density estimation procedure. Next are the naive estimates (no edge effect assumed) of density, produced by dividing the population size estimate by the subgrid area, and the values of parameters necessary to the regression analysis. The estimates of size increase as the grids become larger, but the naive density estimates decrease because the importance of the boundary strip diminishes as the grid size increases. However, we will see that a boundary strip is necessary even with the entire grid. Next, a list of comparisons indicates good agreement between the naive estimates and estimates predicted from the nonlinear regression routine; it is followed by estimates of density and boundary strip width. The estimated density of 64.9 squirrels/ha, which is much smaller than the smallest naive estimate from the total grid, suggests a need to adjust for the edge effect. Such an adjustment, here the addition of a strip 11.8 m wide around the grid, is justified further by the significance of the test for nonzero strip width ($P < 0.01$). From the estimated standard errors for the density and strip width estimates also provided, we see that the density estimate is not especially precise ($cv = 16\%$), nor is the approximately 95% confidence interval of 44.5-85.4 very narrow. Use of a larger grid probably would have increased the precision. (See Chapter 7 for recommendations regarding grid size.)

Biologists interested in running program CAPTURE to obtain density estimates may be interested in the following information. The data matrix X_{ij} was read by using TASK READ CAPTURES. (Only XY REDUCED or XY COMPLETE data formats are allowed because the trap coordinates are necessary.) TASK UNIFORM DENSITY TEST produced Fig. 6.7b.

Model M_{bh} was selected by using the output from TASK MODEL SELECTION, although Model M_{tbh} was ranked highest because of an apparently high probability of capture on day 3.

The density estimation method is called by TASK DENSITY ESTIMATE and starts with the four naive density estimates (Figs. 6.7c-6.7f), the covariance matrix expressing the degree of overlap among the nested grids, the coefficients A(I) and B(I), and the starting values provided by the user. In this example, 59 iterations were required to maximize the multiple correlation coefficient to within a small tolerance value. The procedure simultaneously estimates D and W. It can not be performed on a hand calculator because of the large amount of computation required. Additional details on program CAPTURE are given in *White et al. (1978)*.

The data set is too inadequate for the performance of the test

```
CHAPTER 6 EXAMPLE 6

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

        EXPECTED VALUES TOO SMALL.  TEST NOT PERFORMED.

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

        CHI-SQUARE VALUE =    0.722   DEGREES OF FREEDOM =   1   PROBABILITY OF LARGER VALUE =  0.39557

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 =    2.777   DEGREES OF FREEDOM =   4   PROBABILITY OF LARGER VALUE =  0.59572

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 =    3.289   DEGREES OF FREEDOM =   4   PROBABILITY OF LARGER VALUE =  0.51069
```

The test statistics may not be closely approximated by chi-square distributions due to small sample size (see Fig. 2.12)

```
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 =    1.416   DEGREES OF FREEDOM =   5   PROBABILITY OF LARGER VALUE =  0.92254

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

        CHI-SQUARE VALUE =    0.678   DEGREES OF FREEDOM =   2   PROBABILITY OF LARGER VALUE =  0.71233

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

        CHI-SQUARE VALUE =    0.738   DEGREES OF FREEDOM =   3   PROBABILITY OF LARGER VALUE =  0.86431

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

        EXPECTED VALUES TOO SMALL.  TEST NOT PERFORMED.

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 =    6.125   DEGREES OF FREEDOM =   2   PROBABILITY OF LARGER VALUE =  0.04677

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   1.00     0.81     0.37     0.64     0.00     0.17     0.35     0.73
```

The data are again inadequate for computation of the test

```
APPROPRIATE MODEL PROBABLY IS M(O)
SUGGESTED ESTIMATOR IS NULL.
```

Due to small sample size, the tests do not have much power for detecting the sources of unequal catchability, and thus the model selection procedure defaults to Model M_o

Fig. 6.6b. Output from the model selection procedure.

CHAPTER 6 EXAMPLE 6

```
NUMBER OF TRAPPING OCCASIONS WAS              5
NUMBER OF ANIMALS CAPTURED, M(T+1), WAS      24
TOTAL NUMBER OF CAPTURES, N., WAS            79

ESTIMATED PROBABILITY OF CAPTURE, P-HAT =  0.6583


POPULATION ESTIMATE IS          24 WITH STANDARD ERROR      0.3429
APPROXIMATE 95 PERCENT CONFIDENCE INTERVAL         23 TO         25
```

A deceptively narrow confidence interval often results from studies in which very few animals are captured, and confidence levels are very much less than the stated level of 95 percent

Fig. 6.6c. Estimation of population size using the null estimator of Model M_o.

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TEST FOR UNIFORM DENSITY. SEE THIS SECTION OF THE MONOGRAPH FOR DETAILS.
CHAPTER 6 EXAMPLE 7

MATRIX OF CAPTURES PER TRAP STATION.

COLUMNS	1	2	3	4	5	6	7	8	9	10
ROW 1	0	2	0	0	0	5	1	2	2	0
ROW 2	3	1	1	0	0	0	0	4	0	4
ROW 3	0	1	2	3	0	1	0	3	0	4
ROW 4	0	2	3	1	0	0	3	1	3	1
ROW 5	2	2	1	0	2	1	1	1	2	3
ROW 6	4	2	3	3	3	0	4	0	3	2
ROW 7	1	0	0	4	3	4	2	4	0	2
ROW 8	5	6	1	4	4	4	0	1	0	0
ROW 9	1	4	3	4	4	4	3	1	0	3
ROW 10	5	5	2	1	1	2	4	2	1	4

Total Grid

Middle Outer Grid

Middle Inner Grid

Inner Grid

A total of 3 animals were caught in this trap during the 5 day trapping period

IN THE ABOVE MATRIX, TRAP COORDINATES ARE ROUNDED TO THE NEAREST WHOLE INTEGER.
IN THE FOLLOWING GOODNESS OF FIT TESTS, TRAP COORDINATES THAT ARE NOT INTEGERS
AND NON-RECTANGULAR TRAPPING GRIDS WILL CAUSE SPURIOUS RESULTS.

Fig. 6.7a. The grid definitions and capture matrix for an estimation of Richardson's ground squirrel density.

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TEST FOR UNIFORM DENSITY. SEE THIS SECTION OF THE MONOGRAPH FOR DETAILS.
CHAPTER 6 EXAMPLE 7

Evidence of nonuniform density in a horizontal (north-south) direction

CHI-SQUARE TEST OF UNIFORM DENSITY BY ROWS.

ROW	1	2	3	4	5	6	7	8	9	10
OBSERVED	12	13	14	14	15	24	20	25	27	27
EXPECTED	19.100	19.100	19.100	19.100	19.100	19.100	19.100	19.100	19.100	19.100
CHI-SQUARE	2.639	1.948	1.362	1.362	0.880	1.257	0.042	1.823	3.268	3.268

TOTAL CHI-SQUARE = 17.85 WITH 9 DEGREES OF FREEDOM. PROBABILITY OF LARGER VALUE = 0.0370

CHI-SQUARE TEST OF UNIFORM DENSITY BY COLUMNS.

COLUMN	1	2	3	4	5	6	7	8	9	10
OBSERVED	21	25	16	20	17	21	18	19	11	23
EXPECTED	19.100	19.100	19.100	19.100	19.100	19.100	19.100	19.100	19.100	19.100
CHI-SQUARE	0.189	1.823	0.503	0.042	0.231	0.189	0.063	0.001	3.435	0.796

TOTAL CHI-SQUARE = 7.27 WITH 9 DEGREES OF FREEDOM. PROBABILITY OF LARGER VALUE = 0.6088

CHI-SQUARE TEST OF UNIFORM DENSITY BY RINGS (OUTER RING IS NUMBER 1).

RING	1	2	3	4	5
OBSERVED	74	50	36	25	6
EXPECTED	68.760	53.480	38.200	22.920	7.640
CHI-SQUARE	0.399	0.226	0.127	0.189	0.352

TOTAL CHI-SQUARE = 1.29 WITH 4 DEGREES OF FREEDOM. PROBABILITY OF LARGER VALUE = 0.8625

Number of animals captured in the eighth column of traps during the trapping period

Fig. 6.7b. Tests of three null hypotheses concerning uniformity of density over the grid.

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POPULATION ESTIMATION WITH VARIABLE PROBABILITY REMOVAL ESTIMATOR. SEE M(BH) OR REMOVAL MODELS OF THE MONOGRAPH FOR DETAILS.
INNER GRID X=4-7 Y=4-7

OCCASION	J=	1	2	3	4	5	
TOTAL CAUGHT	M(J)=	0	4	9	13	16	16
NEWLY CAUGHT	U(J)=	4	5	4	3	0	

K	N-HAT	SE(N)	CHI-SQ.	PROB.	ESTIMATED P-BAR(J),J=1,...,5				
1	17.67	2.873097	3.801	0.2837	0.3454	0.3454	0.3454	0.3454	0.3454
2	16.00	1.022285	3.340	0.1883	0.2500	0.5454	0.5454	0.5454	0.5454
3	16.00	0.5785123	2.198	0.1382	0.2500	0.4167	0.7000	0.7000	0.7000

$\hat{N}_1$

POPULATION ESTIMATE IS 18 WITH STANDARD ERROR 2.8731

APPROXIMATE 95 PERCENT CONFIDENCE INTERVAL 12 TO 24

HISTOGRAM OF U(J)

```
FREQUENCY    4    5    4    3    0
--------------------------------------
     5            *
     4       *    *    *
     3       *    *    *    *
     2       *    *    *    *
     1       *    *    *    *
--------------------------------------
```

Fig. 6.7c. Estimation of population size on the inner grid.

```
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POPULATION ESTIMATION WITH VARIABLE PROBABILITY REMOVAL ESTIMATOR.  SEE M(BH) OR REMOVAL MODELS OF THE MONOGRAPH FOR DETAILS.
MIDDLE INNER GRID X=3-8 Y=3-8


OCCASION          J=     1    2    3    4    5
TOTAL CAUGHT    M(J)=    0   15   19   23   28   29
NEWLY CAUGHT    U(J)=   15    4    4    5    1


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

  1       30.15  1.923854          4.969    0.1741      0.4412  0.4412  0.4412  0.4412  0.4412
  2       32.44  5.616076          3.022    0.2207      0.4625  0.3129  0.3129  0.3129  0.3129
  3       29.49  1.874384          2.727    0.0987      0.5086  0.2760  0.5410  0.5410  0.5410

POPULATION ESTIMATE IS              32 WITH STANDARD ERROR      5.6161

APPROXIMATE 95 PERCENT CONFIDENCE INTERVAL          20 TO          44


HISTOGRAM OF U(J)


FREQUENCY      15    4    4    5    1
-----------------------------------------
EACH * EQUALS     2 POINTS

        16      *
        14      *
        12      *
        10      *
         8      *
         6      *              *
         4      *    *    *    *
         2      *    *    *    *    *
-----------------------------------------
```

$\hat{N}_2$

Average probability of capture of those members of the population not captured on the first occasion

Fig. 6.7d. Estimation of population size on the middle inner grid.

```
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POPULATION ESTIMATION WITH VARIABLE PROBABILITY REMOVAL ESTIMATOR.  SEE M(BH) OR REMOVAL MODELS OF THE MONOGRAPH FOR DETAILS.
MIDDLE OUTER GRID X=2-9 Y=2-9


OCCASION          J=     1    2    3    4    5
TOTAL CAUGHT    M(J)=    0   24   30   35   43   45
NEWLY CAUGHT    U(J)=   24    6    5    8    2

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

  1       47.41  2.633526          8.462    0.0374      0.4284  0.4284  0.4284  0.4284  0.4284
  2       55.12  13.53864          4.022    0.1339      0.4354  0.2373  0.2373  0.2373  0.2373
  3       48.71  5.969894          3.742    0.0531      0.4928  0.2429  0.3935  0.3935  0.3935

POPULATION ESTIMATE IS              55 WITH STANDARD ERROR      13.5386

APPROXIMATE 95 PERCENT CONFIDENCE INTERVAL          28 TO          82


HISTOGRAM OF U(J)


FREQUENCY      24    6    5    8    2
-----------------------------------------
EACH * EQUALS     3 POINTS

        24      *
        21      *
        18      *
        15      *
        12      *
         9      *              *
         6      *    *    *    *
         3      *    *    *    *    *
-----------------------------------------
```

$\hat{N}_3$

Very wide confidence interval

Fig. 6.7e. Estimation of population size on the middle outer grid.

```
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POPULATION ESTIMATION WITH VARIABLE PROBABILITY REMOVAL ESTIMATOR.  SEE M(BH) OR REMOVAL MODELS OF THE MONOGRAPH FOR DETAILS.
TOTAL GRID X=1-10 Y=1-10
```

Good fit of the model to the observed data

```
OCCASION              J=     1     2     3     4     5
TOTAL CAUGHT       M(J)=     0    33    49    62    73    76
NEWLY CAUGHT       U(J)=    33    16    13    11     3

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

   1     82.73   4.642233          3.065     0.3817      0.3865  0.3865  0.3865  0.3865  0.3865
   2     84.17   6.955550          2.713     0.2576      0.3921  0.3593  0.3593  0.3593  0.3593
   3     79.21   3.955951          2.044     0.1528      0.4166  0.3462  0.5033  0.5033  0.5033
```

$\hat{N}_4$

```
POPULATION ESTIMATE IS           83 WITH STANDARD ERROR        4.6422

APPROXIMATE 95 PERCENT CONFIDENCE INTERVAL            73 TO          93
```

Relatively precise estimate

```
HISTOGRAM OF U(J)


FREQUENCY      33     16     13     11      3
------------------------------------------------
EACH * EQUALS      4 POINTS

        32     *
        28     *
        24     *
        20     *
        16     *      *
        12     *      *      *      *
         8     *      *      *      *
         4     *      *      *      *      *
------------------------------------------------
```

Fig. 6.7f. Estimation of population size on the total grid.

```
JOINT ESTIMATION OF DENSITY AND BOUNDARY STRIP WIDTH FROM CAPTURE DATA.  SEE THIS SECTION OF THE MONOGRAPH FOR DETAILS.
CHAPTER 6 EXAMPLE 7

        STARTING VALUES FOR DENSITY ESTIMATION--
        NUMBER OF GRIDS                              4
        TRAP INTERVAL                            10.00
        UNITS CONVERSION                      10000.00
        INITIAL DENSITY ESTIMATE               75.3261
        INITIAL STRIP WIDTH ESTIMATE            8.5581

   GRID  NAIVE DENSITY   PERIMETER/AREA      PI/AREA       STARTING COVARIANCE MATRIX
    I        Y(I)             A(I)             B(I)

    1     200.0000       0.1333333         0.3491E-02    0.102E+04
    2     128.0000       0.8000000E-01     0.1257E-02     353.      505.
    3     112.2449       0.5714286E-01     0.6411E-03     258.      368.      763.
    4     102.4691       0.4444444E-01     0.3879E-03     35.4      50.5      105.      32.8
```

Density will be in terms of animals/hectare

Density estimates from each of the subgrids assuming no edge effect

```
RESULTS OF ITERATIONS
   FUNCTION EVALUATIONS REQUIRED                        65
   ESTIMATED SIGNIFICANT DIGITS OF PARAMETER VALUES      9


        FITTED MODEL COMPARED TO THE DATA
        GRID(I)      Y(I)        F(I)
           1       200.000     198.641
           2       128.000     137.594
           3       112.245     114.520
           4       102.469     102.503
MULTIPLE CORRELATION COFFICIENT IS 0.99421
```

A value close to 1 indicates a good fit of the model to the data

```
ESTIMATED DENSITY=          64.949    10.4286    = ITS STANDARD ERROR
ESTIMATED STRIP WIDTH=      11.796     4.3152    = ITS STANDARD ERROR
CORRELATION OF ESTIMATORS    -.9580

TEST OF ESTIMATED STRIP WIDTH GREATER THAN ZERO.
Z-VALUE =  2.7335   PROBABILITY OF LARGER VALUE =   0.0031
```

Indication that addition of a strip width is necessary to compensate for edge effects

```
           FINAL COVARIANCE MATRIX

        1019.
        380.3      504.6
        289.2      383.8      763.4
        40.72      54.04      107.5      32.85
```

Fig. 6.7g. Output from the density estimation algorithm.