CHAPTER 5
DENSITY ESTIMATION

Previous chapters in this primer have dealt only with the problem of estimating population size N. The only assumption made about the area to which N applies is that its size is finite.

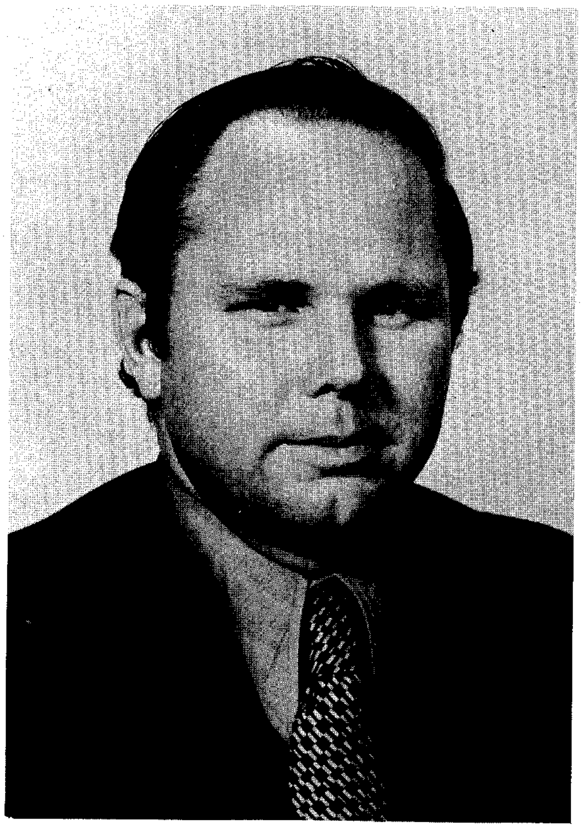
Density D is defined as the number of animals per unit of area. Density estimation extends population size estimation to include an estimate of the area to which the population estimate $\hat{N}$ relates. To estimate density, the assumption of demographic closure still must be met. That is, N must be reasonably constant over the time interval in which capture-recapture data are collected. Thus, animals cannot be immigrating to or emigrating from the area, and no death or recruitment is allowed. These assumptions concerning closure have been made throughout this primer. In the present discussion, we also assume that traps have been placed in a square or rectangular grid design.

Density estimation is not as simple as dividing $\hat{N}$ by the area (A) of the trapping grid, because of the phenomenon known as "edge effect." For example, animals at the edge of a grid will not spend all of their time on the grid, because the grid area contains only part of their home range. Thus, the effective area trapped is somewhat larger than the grid area (Fig. 5.1), because the area to which $\hat{N}$ applies includes the entire home ranges of such animals. Hence, the naive density estimate $\hat{D} = \hat{N}/A$ will tend to overestimate D, because A does not include the additional area around the grid boundary, called the boundary strip. In Fig. 5.2, the grid is very large relative to the home range, and thus the area of the edge effect is almost negligible relative to the size of the grid. In contrast, Fig. 5.3 represents the opposite situation: the grid is very small relative to the home range. In this situation, a valid density estimate probably cannot be obtained.

Biologists have been aware of this potential source of bias for many decades *(Dice 1938, 1941; Stickel 1954)* and have proposed several approaches for handling the problem. Perhaps the most frequently used approach is based on Dice's suggestion that the width of the boundary strip (W) be taken as one-half the average diameter of the home range of the species. Suggestions for estimating this diameter from the trapping data have been made by several authors *(Hayne 1949b; Stickel 1954; Tanaka 1972; Otis et al. 1978:72-73)*, but the approaches are all subject to difficulties. For example, the estimates depend on trap spacing and numbers of recaptures. A second approach involves the use of assessment lines *(M. H. Smith et al. 1971, 1975; H. D. Smith et al. 1972; Swift and Steinhorst 1976; O'Farrell et al. 1977)*. Although this approach has produced good results, the method can become quite complex and is heavily dependent on the design of the trap layout. Our discussion here focuses on a third approach, which depends on jointly estimating density and boundary strip width by using data from selected subgrids *(Otis et al. 1978:67-74)*.

Theory

The key concept in this approach to estimating the boundary strip W of a trapping grid is that the importance of the boundary strip decreases as the size of the grid increases. To illustrate, consider a square with each side 5 units long. If a strip 1 unit wide is added all around (with corners rounded to quarter circles), the area is increased by 93%. However, if the grid is 50 units on each side, the increase in area owing to the addition of a 1-unit strip is only 8% (Fig. 5.4). Hence, the naive estimate of density for a species whose home range radius is on the order of 1 unit would have a large bias for the 5 by 5 grid, but the same estimate would have a small bias for a 50 by 50 grid.



Michael Smith

Michael Smith received his Ph.D. degree from the University of Florida in 1966. He worked on the population biology of mice in old fields, in the sandy soils of the southeastern United States, where the mice can be dug out of burrows easily. This technique allowed independent estimates of population characteristics in addition to those derived from classic trapping approaches. The realization that strong biases are inherent in trapping data has influenced his approach to study of the population biology of vertebrates since that time.

Smith joined the staff of the Savannah River Ecology Laboratory at the University of Georgia in 1966 and shortly thereafter became involved in the International Biological Program (IBP). Estimates of density, not just population numbers, were a critical part of this program because calculations of energy flow and elemental cycling require density values. Most of his work for the IBP, conducted in conjunction with John B. Gentry, involved the use of techniques to estimate the size of the sampling area. Assessment lines and "radioactive trap nights" were investigated in efforts to determine the best methods for obtaining density estimates and confidence intervals for small mammal populations.

Smith's current interests lie with the genetic regulation of population processes. Animal population density is one of the most important variables in this field, as it is in most fields that have occupied his interests. Smith is now Director of the Savannah River Ecology Laboratory. (Recent photograph.)

Program CAPTURE estimates W and D from a single trapping grid by constructing a set of nested grids (Fig. 5.5). The naive estimate of density for each grid is

$$\hat{Y}_i = \hat{N}_i/A_i, \qquad i = 1, \ldots, k;$$

that is, the population estimate for the i^{th} grid, $\hat{N}_i$, divided by the area of the i^{th} grid, A_i. Clearly, $\hat{Y}_1$, which corresponds to the innermost grid, has the most bias, and $\hat{Y}_k$ probably has the least, because of the decrease in importance of strip width as grid size increases.

To demonstrate this phenomenon, we will consider the (unpublished) data of Burnham and Cushwa,* discussed in *Otis et al. (1978:36-37).* Showshoe hares *(Lepus americanus)* were trapped in a black spruce forest 48 km north of Fairbanks, Alaska. A 10 by 10 live-trapping grid was used, with traps spaced 200 ft (61 m) apart. Because the traps were not baited for the first 3 days, only the data from the last 6 days appear here. The model selection procedure chose Model M_h as the appropriate model, so the jackknife estimator is used.

The area A_1 of the inner, 4 by 4 grid is 360 000 ft^2, and the population estimate is 31 animals. Thus, the naive estimate of density $\hat{Y}_1$ is 3.8 hares per acre. Similarly, for the next larger, 6 by 6 grid, the population estimate is 44 hares and the naive estimate of density $\hat{Y}_2$ is 1.9 hares per acre. The naive estimates of density for the 8 by 8 and 10 by 10 grids are $\hat{Y}_3$ = 1.6 and $\hat{Y}_4$ = 1.2 hares per acre, respectively. The estimates trend downward (from 3.8 to 1.2) because the additional strip width around the grid becomes less and less important as the grid size increases.

*K. P. Burnham and C. Cushwa, US Fish and Wildlife Service.

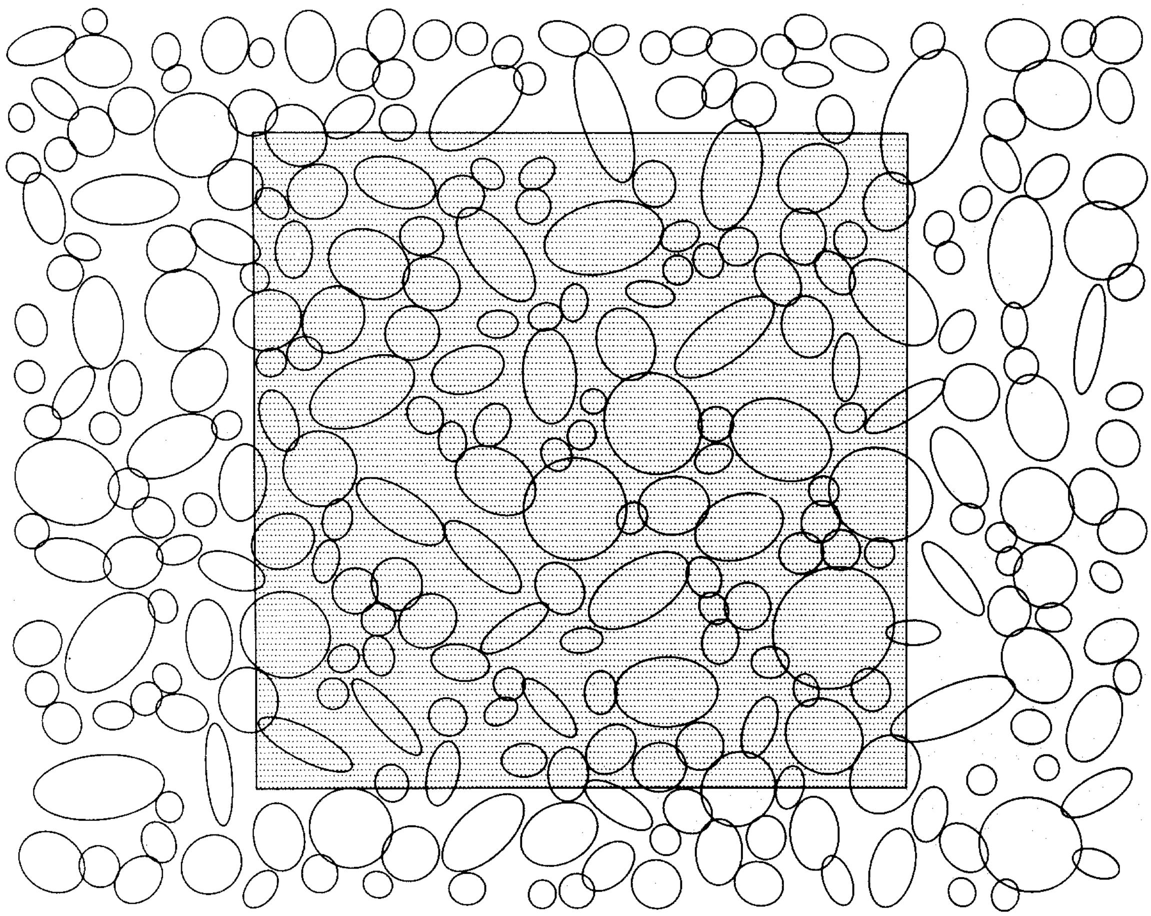


Fig. 5.1. The trapping grid (shaded area) includes all, part, or none of the home ranges (ellipses) of the animals in the vicinity of the grid. Some of the animals whose home ranges overlap the grid will be captured, and thus the effective area of the trapping grid is larger than its physical size, necessitating a technique to estimate the effective grid area and density at the same time. Note that some of the home ranges do not overlap the trapping grid, and hence the animals belonging to these ranges are not captured.

The statistical treatment of the estimation method is given in *Otis et al. (1978:69-72, 121-122).* Briefly, it is assumed that some fixed but unknown strip width W surrounds each of the k subgrids (Fig. 5.6), and an equation is derived that relates the naive density estimates $\hat{Y}_i$ to D and W. A complicated statistical approach known as the generalized nonlinear least-squares method uses this basic relation to derive the estimates. The estimates $\hat{D}$ and $\hat{W}$ are derived so that the sum of squared differences between the naive estimates Y_i and the predicted values is minimized.

Example

This illustration of the density estimation procedure is based on a set of capture data* collected on Richardson's ground squirrel (*Spermophilus richardsoni*) inhabiting rangeland near Kremmling, Colorado. A 10 by 10 grid with 10-m trap spacing was established in June and trapped for 6 consecutive days. Figures 5.7a and b give the numbers of captures at each trap during this period and the results of three simple chi-square tests, each of which tests a hypothesis concerning the uniformity of ground

*The data, unpublished, are from K. Fagerstone, US Fish and Wildlife Service.

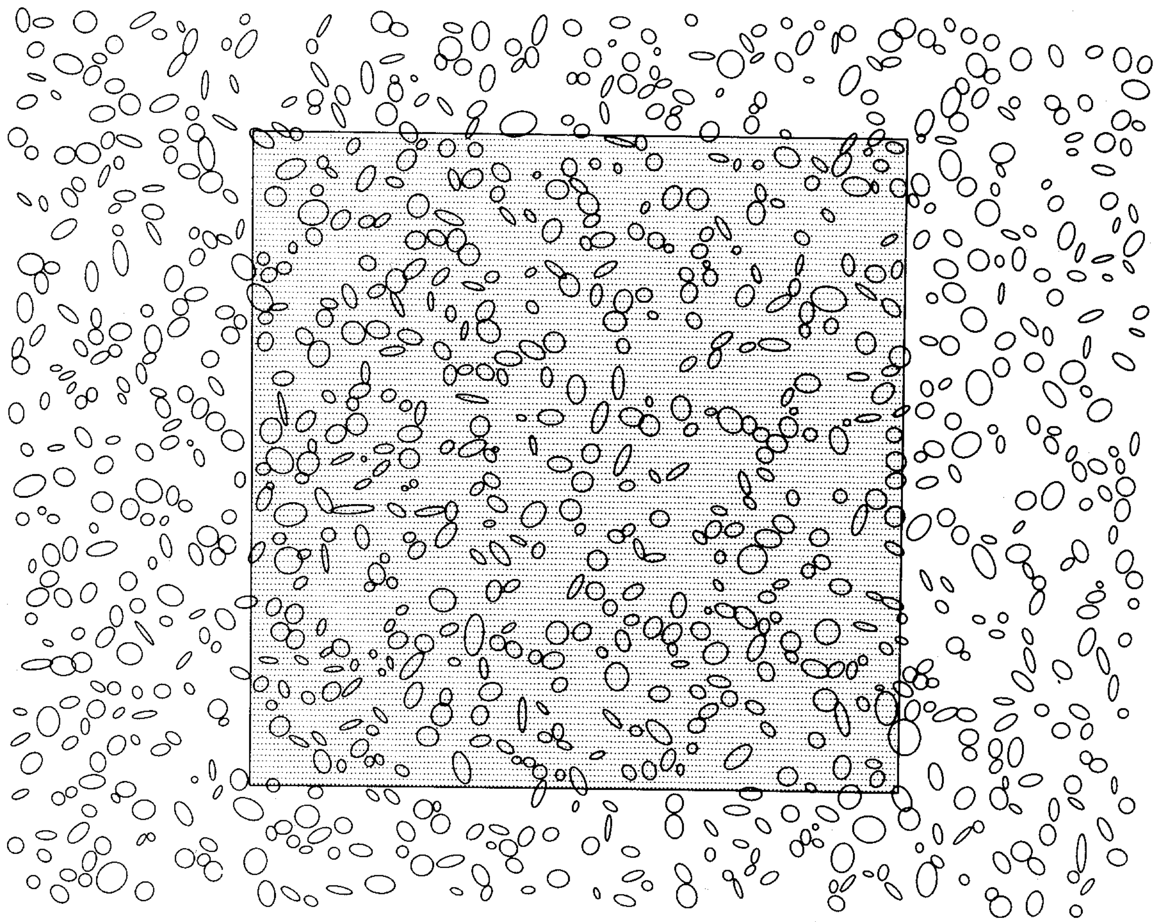


Fig. 5.2. Here the trapping grid (shaded area) is much larger relative to home range size than in Fig. 5.1. Therefore, the effective area of the trapping grid probably is little, if any, larger than its physical size.

squirrel density over the grid. A uniform density has been assumed in the derivation of the estimation method and, therefore, we do not wish to see a rejection of the uniformity hypothesis in any of the tests. The data set gives no evidence of nonuniformity, because none of the tests approach significance. We are not yet sure how severely the estimation method would be affected if the uniform density condition were not met (see Chapter 6, Example 7), but we can assume safely that accuracy would be decreased. If density is not uniform, defining the concept of parameter D becomes difficult.

Figures 5.7c-f give the results of population estimation for each of the four subgrids. The estimator for Model M_{bh} has been used in each case because this is the model chosen by the model selection procedure for the entire data set. Although relatively few squirrels were captured in the inner and middle inner grids, the high capture success indicated by the p_j estimates provides sufficient confidence in the reliability of the population estimates for these grids. Furthermore, in all four subgrids, the model provided a good fit to the data, as indicated by the chi-square and probability columns in the output.

Figure 5.7g gives the basic results of the density estimation procedure. Listed first are the values of necessary parameters and the starting values for density D and strip width W. (*Otis et al. 1978:121-122* gives the derivation of the starting values.) The next information of interest compares the naive estimate of density for each subgrid (that is, the population estimate divided by the area of the subgrid, $\hat{Y}_i = \hat{N}_i/A_i$) with the values predicted by the fitted nonlinear least-squares regression equation. This output gives the experimentor a feel for how well the regression model fits the data, and the multiple correlation coefficient provides a quantitative measure of the model's adequacy. The coefficient's value in this example, R =

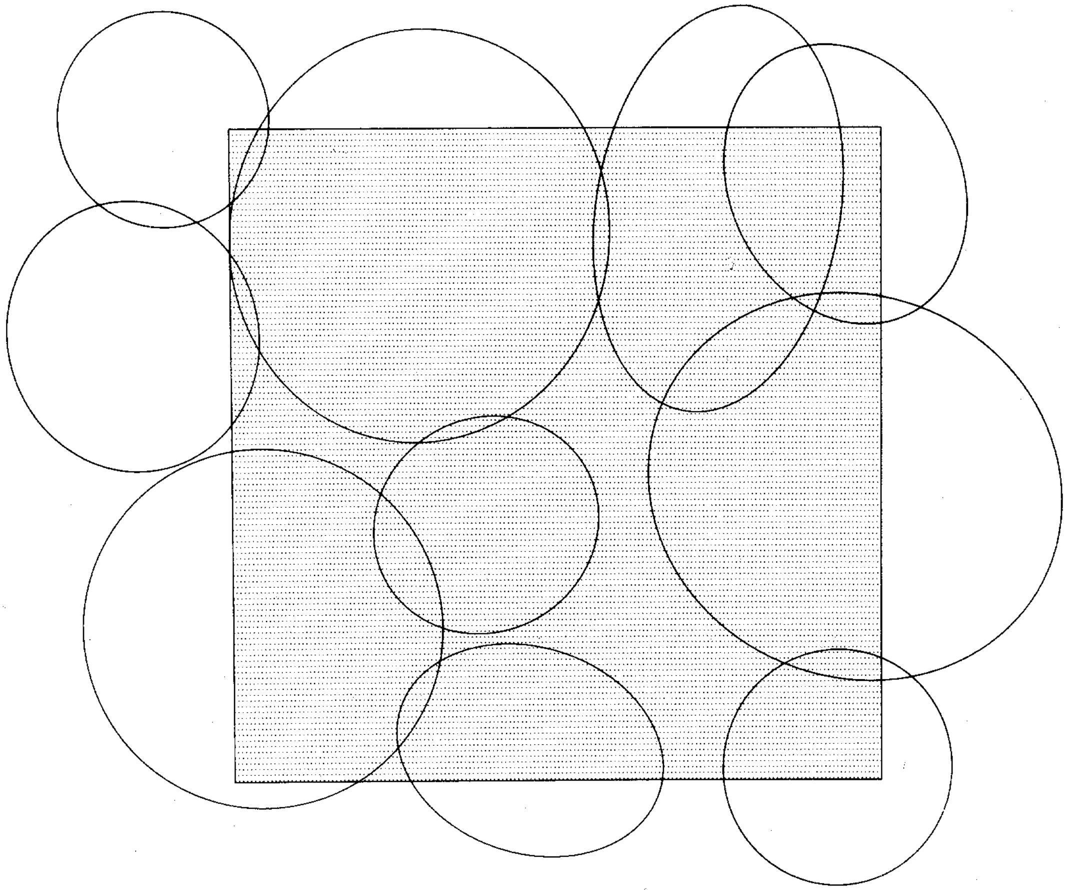


Fig. 5.3. Because almost all of the home ranges (ellipses) include some area outside the trapping grid (shaded area), the grid's effective area is much larger than its physical area. At best, a very poor density estimate would be achieved under these circumstances.

0.93169, indicates that the regression equation has accounted for about 93% of the variation in the naive estimates $\hat{Y}_i$. Next, estimates of the parameters D and W and their standard errors are given. From this capture-recapture experiment, program CAPTURE estimates that D equals about 44 ground squirrels per hectare. The estimate depends on the estimate of W, that is, on the fact that a strip of estimated width 12.4 m must be added to all four sides of the physical grid area to account for the larger effective grid area. The output also provides an estimate of the correlation between the estimates of D and W. Intuitively, we expect a high negative correlation because the larger the strip width (the effective area trapped), the lower the density estimate should be. Our estimate of –0.9805 indicates such a relation. Finally, program CAPTURE calculates a simple test of the hypothesis that W is significantly different from zero—that the data justify the addition of a strip width. Our results show that such an addition is indeed necessary.

Design Requirements

The density estimation procedure requires that the following assumptions be met if the data are to be analyzed by program CAPTURE.

1. All the assumptions made earlier in this text continue to be met, because a population estimate must be made for each of the nested grids.

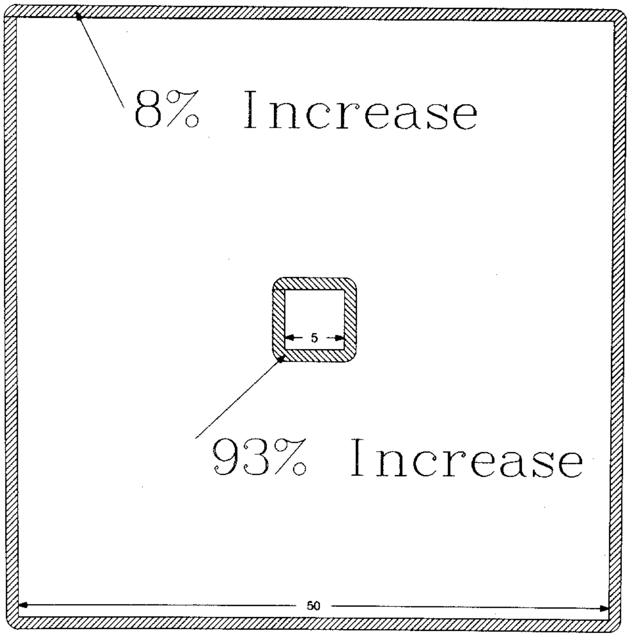


Fig. 5.4. The relative importance of a fixed-width boundary strip decreases as the grid size increases. Thus, the addition of a 1-unit-wide boundary strip to a 5- by 5-unit trapping grid adds 93% to the grid's effective size. In contrast, the addition of the same width boundary strip to a 50- by 50-unit trapping grid adds only 8% to the larger grid's effective size.

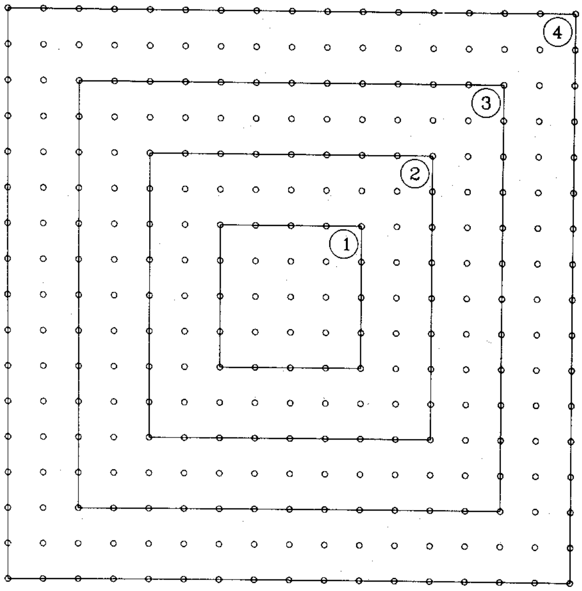


Fig. 5.5. The effect of boundary strip width on density is determined by program CAPTURE from nested subgrids within the entire grid. Thus, the outer grid (4) consists of all the traps, with x = 1 – 17 and y = 1 – 17, and the smallest inner grid (1) consists of only the traps x = 7 – 11 and y = 7 – 11. Because the impact of the strip width decreases with increasing grid size (Fig. 5.4), the nested grid structure provides a means of estimating strip width. The naive density estimates should decrease as the grid size increases; that is, the naive estimate of density ($\hat{Y}_1$) for Grid 1 is expected to be larger than the naive estimate of density ($\hat{Y}_4$) for Grid 4.

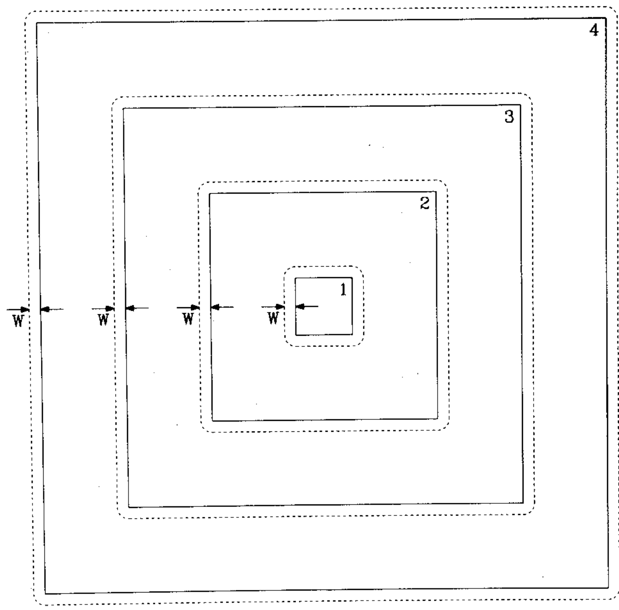


Fig. 5.6. The boundary strip width W is assumed to be constant, regardless of the grid size. The nested subgrids are used to construct an estimate of W in program CAPTURE.

MARK-RECAPTURE POPULATION AND DENSITY ESTIMATION PROGRAM DEVELOPED BY THE UTAH COOPERATIVE WILDLIFE RESEARCH UNIT. PAGE 701
CAPTURE RECAPTURE WORKBOOK EXAMPLES PROGRAM VERSION OF MAY 07, 1980 80/07/26.

TEST FOR UNIFORM DENSITY. SEE THIS SECTION OF THE MONOGRAPH FOR DETAILS.
CHAPTER 5 DENSITY ESTIMATION EXAMPLE

MATRIX OF CAPTURES PER TRAP STATION.

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

Grid Number

4 Entire grid x=1-10 y=1-10
3 Middle outer grid x=2-9 y=2-9
2 Middle Inner grid x=3-8 y=3-8
1 Inner grid x=4-7 y=4-7

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. 5.7a. Nested subgrids used in the density estimation procedure with data on Richardson's ground squirrels. In the matrix, each entry is the number of ground squirrels caught at a particular trap station.

MARK-RECAPTURE POPULATION AND DENSITY ESTIMATION PROGRAM DEVELOPED BY THE UTAH COOPERATIVE WILDLIFE RESEARCH UNIT. PAGE 702
CAPTURE RECAPTURE WORKBOOK EXAMPLES PROGRAM VERSION OF MAY 07, 1980 80/07/26.

TEST FOR UNIFORM DENSITY. SEE THIS SECTION OF THE MONOGRAPH FOR DETAILS.
CHAPTER 5 DENSITY ESTIMATION EXAMPLE

CHI-SQUARE TEST OF UNIFORM DENSITY BY ROWS.

ROW	1	2	3	4	5	6	7	8	9	10
OBSERVED	8	12	10	7	10	10	15	16	14	18
EXPECTED	12.000	12.000	12.000	12.000	12.000	12.000	12.000	12.000	12.000	12.000
CHI-SQUARE	1.333	0.000	0.333	2.083	0.333	0.333	0.750	1.333	0.333	3.000

TOTAL CHI-SQUARE = 9.83 WITH 9 DEGREES OF FREEDOM. PROBABILITY OF LARGER VALUE = 0.3641

CHI-SQUARE TEST OF UNIFORM DENSITY BY COLUMNS.

COLUMN	1	2	3	4	5	6	7	8	9	10
OBSERVED	9	13	10	22	13	10	14	12	11	6
EXPECTED	12.000	12.000	12.000	12.000	12.000	12.000	12.000	12.000	12.000	12.000
CHI-SQUARE	0.750	0.083	0.333	8.333	0.083	0.333	0.333	0.000	0.083	3.000

TOTAL CHI-SQUARE = 13.33 WITH 9 DEGREES OF FREEDOM. PROBABILITY OF LARGER VALUE = 0.1481

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

RING	1	2	3	4	5
OBSERVED	38	39	25	18	0
EXPECTED	43.200	33.600	24.000	14.400	4.800
CHI-SQUARE	0.626	0.868	0.042	0.900	4.800

TOTAL CHI-SQUARE = 7.24 WITH 4 DEGREES OF FREEDOM. PROBABILITY OF LARGER VALUE = 0.1240

None of the circled significance values are less than 0.05

Fig. 5.7b. Chi-square tests of uniform density with data on Richardson's ground squirrels. If any of the three probability levels are small ($p < 0.05$), the investigator must question whether the assumption of uniform density across the grid is met.

2. The trapping grid is square or rectangular with the intertrap distance the same in both "row" and "column" directions. Note in Fig. 5.5 that the traps are equally spaced in a lattice.
3. The total trapping grid is large enough to contain at least three, but preferably four, subgrids (including the total grid), as shown in Fig. 5.5. It is not absolutely necessary that each subgrid be increased by two rings of traps as shown, but the greater the relative increase in area to the boundary strip, the better the estimation procedure will work. If additional grids were inserted in Fig. 5.5, the estimate probably would be more precise.
4. The population density is approximately constant in the area of trapping. That is, there is no marked trend in density across the grid. The presence of a trend breaks down the concept of a constant strip width around each nested grid, shown in Fig. 5.6.
5. Trapping success is high. By implicit assumption, a large proportion of the animals are captured and recaptured, because the population estimates $\hat{N}_i$ from each of the subgrids must be reasonably reliable if the method is to work well.

In addition, the coordinates of the trap location of each capture and recapture must be recorded. The (x, y) coordinates of the traps must be known so that population estimates for the various subgrids can be calculated. Thus, if an animal is captured at three locations, but only two of these locations are in the inner subgrid, only these two captures can be used for estimation in the inner subgrid. Additional details about data recording are given in Chapter 7, Study Design.

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	6	
TOTAL CAUGHT	M(J)=	0	3	4	10	13	13	13
NEWLY CAUGHT	U(J)=	3	1	6	3	0	0	

K	N-HAT	SE(N)	CHI-SQ.	PROB.	ESTIMATED P-BAR(J),J=1,..., 6					
1	13.81	2.01375[illegible]	12.974	0.0047	0.3261	0.3261	0.3261	0.3261	0.3261	0.3261
2	13.00	1.012297	10.912	0.0122	0.2308	0.4545	0.4545	0.4545	0.4545	0.4545
3	13.00	0.2028692	1.631	0.4424	0.2308	0.1000	0.7500	0.7500	0.7500	0.7500
4	13.00	0.4201734E-05	0.001	0.9814	0.2308	0.1000	0.6667	0.9998	0.9998	0.9998

POPULATION ESTIMATE IS 13 WITH STANDARD ERROR 0.2029

APPROXIMATE 95 PERCENT CONFIDENCE INTERVAL 12 TO 14

$Y_1 = 13/(30\ m \cdot 30\ m \cdot 1\ ha/10000\ m^2)$
$= 144.44$ animals/ha

HISTOGRAM OF U(J)

```
FREQUENCY     3    1    6    3    0    0
---------------------------------------------
     6                  *
     5                  *
     4                  *
     3        *         *    *
     2        *         *    *
     1        *    *    *    *
---------------------------------------------
```

Fig. 5.7c. An example of population estimation using the generalized removal estimator for Model M_{bh} with data on Richardson's ground squirrels taken from Grid 1 (inner grid) of Fig. 5.7a (x = 4 – 7, y = 4 – 7). The first of four naive density estimates is produced from the population estimate for this grid.

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	6	
TOTAL CAUGHT	M(J)=	0	9	13	21	25	27	28
NEWLY CAUGHT	U(J)=	9	4	8	4	2	1	

K	N-HAT	SE(N)	CHI-SQ.	PROB.	ESTIMATED P-BAR(J),J=1,..., 6					
1	30.85	3.390958	4.084	0.3948	0.3109	0.3109	0.3109	0.3109	0.3109	0.3109
2	30.19	3.284894	3.976	0.2640	0.2981	0.3395	0.3395	0.3395	0.3395	0.3395
3	28.00	0.9337696	0.393	0.8216	0.3214	0.2105	0.5769	0.5769	0.5769	0.5769
4	28.00	0.8693015	0.422	0.5159	0.3214	0.2105	0.5333	0.6363	0.6363	0.6363

POPULATION ESTIMATE IS 31 WITH STANDARD ERROR 3.3910

APPROXIMATE 95 PERCENT CONFIDENCE INTERVAL 24 TO 38

$Y_2 = 31/(50\ m \cdot 50\ m \cdot 1\ ha/10000\ m^2)$
$= 124$ animals/ha

HISTOGRAM OF U(J)

```
FREQUENCY     9    4    8    4    2    1
---------------------------------------------
     9        *
     8        *         *
     7        *         *
     6        *         *
     5        *         *
     4        *    *    *    *
     3        *    *    *    *
     2        *    *    *    *    *
     1        *    *    *    *    *    *
---------------------------------------------
```

Fig. 5.7d. An example of population using the generalized removal estimator for Model M_{bh} with data on Richardson's ground squirrels taken from Grid 2 (middle inner grid) of Fig. 5.7a (x = 3 – 8, y = 3 – 8). The second naive density estimate is produced from the population estimate for this grid.

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	6	
TOTAL CAUGHT	M(J)=	0	17	27	35	39	43	44
NEWLY CAUGHT	U(J)=	17	10	8	4	4	1	

K	N-HAT	SE(N)	CHI-SQ.	PROB.	ESTIMATED P-BAR(J),J=1,...., 6					
1	46.14	2.446583	1.324	0.8573	0.3799	0.3799	0.3799	0.3799	0.3799	0.3799
2	45.81	2.548772	1.423	0.7000	0.3711	0.3969	0.3969	0.3969	0.3969	0.3969
3	44.68	1.766119	1.458	0.4823	0.3805	0.3612	0.4895	0.4895	0.4895	0.4895
4	44.06	1.288259	1.862	0.1723	0.3858	0.3695	0.4688	0.5925	0.5925	0.5925

POPULATION ESTIMATE IS 46 WITH STANDARD ERROR 2.4466

APPROXIMATE 95 PERCENT CONFIDENCE INTERVAL 41 TO 51

HISTOGRAM OF U(J)

$Y_3 = 46/(70\,m \cdot 70\,m \cdot 1\,ha/10000\,m^2)$
$= 93.88$ animals/ha

```
FREQUENCY     17   10    8    4    4    1
---------------------------------------------
EACH * EQUALS    2 POINTS

    18         *
    16         *
    14         *
    12         *
    10         *    *
     8         *    *    *
     6         *    *    *
     4         *    *    *    *    *
     2         *    *    *    *    *    *
---------------------------------------------
```

Fig. 5.7e. An example of population estimation using the generalized removal estimator for Model M_{bh} with data on Richardson's ground squirrels taken from Grid 3 (middle outer grid) of Fig. 5.7a (x = 2 – 9, y = 2 – 9). The third naive density estimate is produced from the population estimate for this grid.

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

OCCASION	J=	1	2	3	4	5	6	
TOTAL CAUGHT	M(J)=	0	24	38	48	53	57	58
NEWLY CAUGHT	U(J)=	24	14	10	5	4	1	

K	N-HAT	SE(N)	CHI-SQ.	PROB.	ESTIMATED P-BAR(J),J=1,...., 6					
1	59.86	2.124398	1.036	0.9043	0.4169	0.4169	0.4169	0.4169	0.4169	0.4169
2	59.44	2.097676	1.120	0.7721	0.4038	0.4404	0.4404	0.4404	0.4404	0.4404
3	58.51	1.513301	1.103	0.5762	0.4102	0.4057	0.5258	0.5258	0.5258	0.5258
4	58.00	1.113654	1.437	0.2307	0.4138	0.4118	0.5000	0.6250	0.6250	0.6250

POPULATION ESTIMATE IS 60 WITH STANDARD ERROR 2.1244

APPROXIMATE 95 PERCENT CONFIDENCE INTERVAL 55 TO 65

HISTOGRAM OF U(J)

$Y_4 = 60/(90\,m \cdot 90\,m \cdot 1\,ha/10000\,m^2)$
$= 74.07$ animals/ha

```
FREQUENCY     24   14   10    5    4    1
------------------------------------------
EACH * EQUALS    3 POINTS

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

Fig. 5.7f. An example of population using the generalized removal estimator for Model M_{bh} with data on Richardson's ground squirrels taken from Grid 4 (entire grid) of Fig. 5.7a (x = 1 – 10, y = 1 – 10). The fourth naive density estimate is produced from the population estimate for this grid.

```
MARK-RECAPTURE POPULATION AND DENSITY ESTIMATION PROGRAM DEVELOPED BY THE UTAH COOPERATIVE WILDLIFE RESEARCH UNIT.    PAGE 708
CAPTURE RECAPTURE WORKBOOK EXAMPLES                                          PROGRAM VERSION OF MAY 07, 1980    80/07/26.

JOINT ESTIMATION OF DENSITY AND BOUNDARY STRIP WIDTH FROM CAPTURE DATA.  SEE THIS SECTION OF THE MONOGRAPH FOR DETAILS.
CHAPTER 5  DENSITY ESTIMATION EXAMPLE

        STARTING VALUES FOR DENSITY ESTIMATION--
        NUMBER OF GRIDS                          4
        TRAP INTERVAL                        10.00
        UNITS CONVERSION                  10000.00
        INITIAL DENSITY ESTIMATE           66.0122
        INITIAL STRIP WIDTH ESTIMATE        7.1501

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

    1     144.4444       0.1333333        0.3491E-02    5.08
    2     124.0000       0.8000000E-01    0.1257E-02    14.5    184.
    3     93.87755       0.5714286E-01    0.6411E-03    3.11    39.4    24.9
    4     74.07407       0.4444444E-01    0.3879E-03    1.07    13.5    8.55    6.88

RESULTS OF ITERATIONS
   FUNCTION EVALUATIONS REQUIRED                         54
   ESTIMATED SIGNIFICANT DIGITS OF PARAMETER VALUES      6
```

Note the decrease in the naive density estimates with increasing grid size

```
        FITTED MODEL COMPARED TO THE DATA
        GRID(I)       Y(I)        F(I)
           1        144.444     142.398
           2        124.000      97.529
           3         93.878      80.648
           4         74.074      71.879

MULTIPLE CORRELATION COFFICIENT IS 0.93169

ESTIMATED DENSITY=          44.612    2.9981   = ITS STANDARD ERROR
ESTIMATED STRIP WIDTH=      12.409    1.0139   = ITS STANDARD ERROR
CORRELATION OF ESTIMATORS    -.9805

TEST OF ESTIMATED STRIP WIDTH GREATER THAN ZERO.
Z-VALUE = 12.2389  PROBABILITY OF LARGER VALUE =  0.0000

             FINAL COVARIANCE MATRIX

        5.081
        16.41     184.0
        3.762     42.17     24.93
        1.348     15.11     8.930     6.879
```

The final density estimate is even smaller than Y_4

Fig. 5.7g. An example of the joint estimation of density D and strip width W with data on Richardson's ground squirrels, $\hat{D}$ = 44.612 ± 2.998 and $\hat{W}$ = 12.409 ± 1.014. The boundary strip model discussed in the text explains 93% of the variance of the Y(I) (the naive estimates of density from the nested subgrids). Note that the naive density estimate for the entire grid ($\hat{Y}_4$ = 74.07 squirrels/ha), which is the best of the four estimates, is reduced almost by half for the final estimate of D.

Summary

1. Density D is the number of animals per unit of area.
2. Because a portion of the animals trapped on a grid actually have some home range area outside the grid, the effective area of a grid is larger than the physical area.
3. To correct the physical area of a trapping grid to its effective area, a constant strip width, W, is added around the grid perimeter.
4. The importance of the strip width W is much greater for a small grid than for a large grid, and thus a set of nested subgrids partitioned from the entire grid is used by program CAPTURE to estimate D and W, simultaneously.
5. The methods used in program CAPTURE to estimate density make the same assumptions as those used for the population estimators in Chapter 3; in addition, density is assumed to be constant in the area of the trap grid.
6. Because $\hat{D}$ and $\hat{W}$ are highly correlated and because a high variability is associated with density estimation experiments, a large proportion of the population must be captured and recaptured to achieve a reliable estimate of either D or W.

Questions and Exercises

1. Would a 3 by 3 trapping grid be satisfactory for estimating density?
2. If the strip width W is equal to zero, is the population geographically closed? (See Chapter 1 for a discussion of geographical closure.)
3. In Fig. 5.1, what is the population (number of animals) at risk of capture?
4. Which would you recommend, one trap per station and twice the grid size, or two traps per station and half the grid size? Why?
5. If there is a linear gradient in density across the grid, would you suggest using subgrids that consist of halves or quarters of the entire grid? Why?
6. Can density be estimated when 100 traps are laid out in one long line instead of in a 10 by 10 grid? If so, how?
7. Why is the naive density estimate of 74.07 for the entire grid in Fig. 5.7g reduced to the final estimate of 44.61?
8. How do the units of density D differ from those of population N?
9. Why does the estimation of D require more than the X matrix defined in Chapter 1?