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Calculation of Home Range And Density Of Small Mammals

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U. S. DEPARTMENT OF HEALTH, EDUCATION, AND WELFARE

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Introduction

Small mammals such as mice and shrews are difficult to observe directly. Nocturnality, protection by overhanging vegetation, and retirement to nest or burrow upon detection of an approaching human contribute to this difficulty of observation. Mammalogists have been forced to develop techniques of trapping (*1*) in order to explore the biology of such animals. Where traps that capture the animals alive are used, it is generally found that each animal confines its activities to the vicinity of several neighboring traps. This spatial limitation of excursions has become known as home range. Traps are usually relatively sparsely distributed throughout any home range. Even so, many animals are captured. Several methods have been proposed for converting records of captures into estimates of density. Some of these methods ignore the question of the movements of the animals in relation to the trap. Others attempt to utilize home range in the calculation of density, that is, number of animals per unit of area, but lack of a mathematical expression of home range has hampered such attempts.

The task we set ourselves was a dual one. First, we wished to examine home range with the view of selecting an equation which would approximately describe it. Second, we wished to examine the methods of estimating density with particular reference to the role of concepts of home range in making such estimates more logical and precise.* Although we have attempted to take a broad view of these two topics, our principal effort was directed toward those aspects of home range and density that were of particular relevance to the standardized sampling procedure used by the North American Census of Small Mammals, or NACSM (*2*).

Home Range

Basic Nature

The home range of an animal is defined as the area it covers in its day-to-day travels (*3*). An inherent property of the home range is that it is fixed, in the sense that the animal does not wander through a space at random but repeatedly covers the same general area. Attempts to make home range a useful concept have involved arbitrary delimitations of the extent of the home range. Boundaries have been designated by polygons, encompassed by lines drawn between the outermost points of capture or by lines drawn halfway between the outermost points of capture and the next most peripherally located traps.

Hayne, who has reviewed the concept of home range (*4*), was the first to present a logical approach to the problem of the relative frequency with which different portions of the home range are visited by a mammal. As a reference point, he took the mean coordinate point of observation or capture, defined as the "apparent center" of activity within the home range. The distance of each point of capture from its apparent center of activity can thus be calculated for each animal. Hayne then carried the concept of home range one step farther. He calculated an index of the relative frequency with which an animal is found per unit of area at different radii from the ap-

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*This monograph is not intended as a comprehensive review of home range and the calculation of density. We have cited only those references which are particularly cogent to the development of our thesis.

parent center of activity. This index equaled the number of captures at a radius divided by the number of traps available at that radius. These indices showed that the probability of an animal being captured in a particular area of unit size decreased with its distance from the apparent center of activity.

Hayne later presented further but more indirect evidence concerning the phenomenon of home range (*5*, fig. 2). Where traps were set in grids, the mean maximum distance from the apparent center of activity increased with the number of times the animals were captured. This may be restated as indicating that the longer the period of observation, the more likely will the animal be observed at those distant points which it visits infrequently. It is logical to assume that the degree to which an animal interacts with its physical environment, in terms of food consumption for example, is proportional to the time it is present in a given area. Therefore, this new concept of home range developed by Hayne is essentially one of relative intensity of usage of the environment although its measurement is in terms of the relative probability of observation of the animal at different places within the home range.

Source of Data

An extensive set of data on the captures of male harvest mice (*Reithrodontomys*), secured by Brant (*6*), forms the basis of this analysis. Three study plots were located in grassland habitat near Berkeley, Calif. Details of the habitat of these plots are given in the 1950 Annual Report of the North American Census of Small Mammals (*2*, pp. 25–29). The plots were irregularly hexagonal in shape, and each plot encompassed approximately 28 acres.

Trapping stations were so distributed as to form a 50-foot grid over each plot. Only one-seventh of the trapping stations were in operation at any one time. Each activated station contained two traps. These activated stations were in groups of four, one at each corner of a square, each side of which measured 50 feet. The minimum distance between the centers of activated groups was 280 feet. At regular intervals all eight traps in each activated group were inspected. Captured animals were marked and released or, if already marked, their number designations were noted prior to release. Then the traps were moved to an adjoining group of stations. By systematically shifting the traps, the entire plot was sampled after seven shifts (*6*).

The distance separating the groups of traps was great enough that most animals had an extremely low probability of exposure to all but one group of traps at any one time. Because of their sparse distribution, the traps only slightly hindered the movement of the mice. Such a situation is desirable for, as Hayne (*5*) has demonstrated, the mean distance of capture from the apparent center of activity decreases as the traps become more dense.

The data initially selected for study were limited to males for which (*a*) there were 3 or more captures (median=8 captures), and (*b*) less than 25 percent of the captures were on the peripheral trapping stations. One hundred and fifteen animals met these specifications. The apparent center of the home range was calculated for each animal, as well as the distance, r, in feet of each capture from the apparent center of activity.

$$r_n=[(x_n-\bar{x})^2+(y_n-\bar{y})^2]^{1/2} \qquad [1]$$

where

$(\bar{x}, \bar{y})$ is the center of the home range

and

(x_n, y_n) is the position of the nth capture.

Expressed as a Density Function

In home range studies, "density function" is a mathematical expression representing the probability of an animal being present in some arbitrarily small area.

From the discussion of concepts of home range, three assumptions are made:

- The home range is fixed. In other words, the statistics of the home range are stationary, or time independent.
- There is a true center of activity although the apparent center of activity may deviate from it.
- The probability of an animal being in a unit of area decreases with increasing distances from the true center of activity. This and the second assumption suggest a bivariate normal

distribution of the density function (7, fig. 3, ch. 6).

$$f(x,y)dxdy=\frac{1}{2\sigma^2\pi}\,e^{-(x^2+y^2)/2\sigma^2}dxdy \qquad [2]$$

where σ is the standard deviation of the distances in the x and y direction and is assumed to be equal for both, and x and y are measured from their respective means. This density function may be used to represent the percentage of time spent in the area $dxdy$ located at the Cartesian coordinates x, y,
or, in polar coordinates

$$f(r,\theta)rd\theta dr=\frac{1}{2\sigma^2\pi}\,e^{-r^2/2\sigma^2}rd\theta dr \qquad [3]$$

Here the area $rd\theta dr$ is determined by r.

There are an unlimited number of equations which would fulfill the requirements of the second and third conditions. The bivariate normal distribution given in equations 2 and 3 is one such function. We shall examine the home range data for male harvest mice to see how well they are approximated by this equation although we are primarily interested in the radial frequency distribution of the average animal.

The density function in terms of the Cartesian coordinates is more meaningful from an ecological standpoint because it states in comparative terms the amount of time spent by an animal in a small standard area at any position in the home range. However, for the initial mathematical manipulation it was found more convenient to express the density function in terms of polar coordinates. Then the probability of finding the animal between the radii r and $r+dr$ about the true center of the home range is

$$f(r)dr=\frac{2}{2\sigma^2}\,e^{-r^2/2\sigma^2}rdr \qquad [4]$$

If equation 4 is integrated over the range 0 to σ we have

$$\int_o^{\sigma}\frac{2r}{2\sigma^2}e^{-r^2/2\sigma^2}dr=1-e^{-\frac{1}{2}}=0.3940 \qquad [5]$$

In the above equations σ, the standard deviation of the normal distribution function, is the value of a radius within which the probability of the animal being present is 39.4 percent if its movements can be described by a bivariate normal density function.

Similarly, integrating equation 4 over the range 0 to 2 σ gives

$$1-e^{-4/2}=0.8645 \qquad [6]$$

Similarly, integrating equation 4 over the range 0 to 3 σ gives

$$1-e^{-9/2}=0.9888 \qquad [7]$$

When the recapture data are contaminated by inclusion of animals which have shifted their home range, that is, those animals with nonstationary home ranges, the observed frequency distribution will include too many captures at longer radii. This will lead to an overestimate of the dimensions of the home range. An examination of the field maps of the home ranges of those 115 males included in the initial group of mice selected for this study revealed that certain individuals had definitely shifted the center of their home range. In the more obvious of these shifts the initial group of captures formed a clump no more than 300 feet in diameter, while the later captures formed a similar clump several hundred feet away. In

Table 1. Home range parameter σ for 25 male harvest mice

Mouse No.	Number captures	σ [1] (feet)	Number days between first and last capture
2298	10	44. 9	88
4053	10	34. 6	109
309	10	53. 5	139
277	10	47. 9	76
100	10	[2] 77. 5	237
278	10	42. 5	84
C1–62	10	69. 2	86
380	11	59. 5	145
369	11	32. 5	133
242	11	60. 0	115
286	12	43. 5	172
403	12	36. 8	137
527	12	60. 0	261
C1–58	13	32. 5	177
C1–18	14	50. 8	106
C1–3	14	68. 5	131
T–7	14	61. 5	218
256	15	[3] 52. 5	174
C1–46	16	71. 2	107
149	16	53. 4	201
393	19	[4] 32. 2	137
284	21	47. 3	165
T–98	21	40. 1	205
C1–16	22	55. 5	172
C1–25	24	57. 7	157

[1] See equation 9a. [2] Maximum. [3] Median.
[4] Minimum.

the light of our hypothesis of a stationary home range, we thought it wise to exclude animals which had definitely exhibited such shifts. The criteria for assembling a more homogeneous group were as follows:

- Animal must have been captured 10 or more times.
- No obvious shifts in home range; that is, a straight line separating the later captures from the earlier ones could not be drawn on the field map.

Twenty-five male mice met these criteria, and they provided 348 capture records, *r*'s (table 1). These records showed no detectable shift in the center of home range.

When it can be assumed that the same bivariate normal distribution given by equation 2 holds for all animals, then the best estimate, s, of σ, based on the maximum likelihood estimate of σ^2 is:

$$s=\left[\frac{\sum_{i=1}^{n}\sum_{j=1}^{K_i}\left\{(\overline{x}_i-x_{ij})^2+(\overline{y}_i-y_{ij})^2\right\}}{2(N-n)}\right]^{1/2} \qquad [8a]$$

where: K_i=number of captures of ith animal

n=number of animals

N=total captures$=\sum_{i=1}^{n} K_i$

$\overline{x}_i=\frac{1}{K_i}\sum_{j=1}^{K_i} x_{ij}$ and $\overline{y}_i=\frac{1}{K_i}\sum_{j=1}^{K_i} y_{ij}$

y_{ij} and x_{ij}=position of ith animal on jth capture

For the 25 male harvest mice σ was estimated to be 52.7 feet. An estimate, s_i, of σ was also made for each mouse (table 1):

$$s_i=\left[\frac{\sum_{j=1}^{K_i}\left\{(\overline{x}_i-x_{ij})^2+(\overline{y}_i-y_{ij})^2\right\}}{2(K_i-1)}\right]^{1/2} \qquad [9a]$$

For many purposes in which the ascertaining of home range is useful, the σ of the recapture radii may be obtained by direct use of the radii. In this procedure the map of the area studied is laid out on a large sheet of graph paper that is finely spaced with vertical and horizontal lines. An overall set of coordinates is established on this grid and points of capture for each animal are plotted. At the termination of observation the mean coordinate point of capture for each animal is recorded on the graph paper and recapture radii are measured directly from this point with a ruler. For practical usages, such as in the calculation of density (equation 51), the σ calculated from such estimated radii are probably accurate enough to justify the time saved in calculation. Equations 8a and 9a become:

$$s=\left[\frac{\sum_{i=1}^{n}\sum_{j=1}^{Ki} r_{ij}^2}{2(N-n)}\right]^{1/2} \qquad [8b]$$

$$s_i=\left[\frac{\sum_{j=1}^{K_i} r_j^2}{2(K_i-1)}\right]^{1/2} \qquad [9b]$$

Equations for σ 8a, 9a, 8b, and 9b take into account the fact that distances are measured from apparent rather than true centers, and the squares of these σ's are unbiased estimates of the parameter appearing in equation 4.

Likelihood ratio methods (*8*, p. 270) were used to test certain assumptions concerning the home range of male harvest mice.

Since the complete bivariate normal distribution contains another parameter, ρ_{xy}, the correlation between the x and y coordinates, and since we wrote equation 2 with $\rho_{xy}=0$, we test this assumption jointly in test I and separately in test III. The other tests are obvious.

Test I. The hypothesis was that $\rho_{xy}=0$, $\sigma^2_x=\sigma^2_y$, for the normal bivariate distribution of captures within an animal

where:

$$-2\log_e\lambda=K_i\log_e(1-r^2)+K_i\log_e\frac{(s_x+s_y)^2}{4s_xs_y} \qquad [10]$$

$$s_x=\sum_{j=1}^{K_i}(x_j-\overline{x})^2 \qquad [11]$$

$$s_y=\sum_{j=1}^{Ki}(y_j-\overline{y})^2 \qquad [12]$$

$$r^2=\frac{\left[\sum_{j=1}^{K_i}(x_j-\overline{x})(y_j-\overline{y})\right]^2}{\sum_{j=1}^{K_i}(x_j-\overline{x})^2\sum_{j=1}^{K_i}(y_j-\overline{y})^2} \qquad [13]$$

Assumption: $x-\bar{x}$ and $y-\bar{y}$ are distributed normally with the parameters σ^2_x, σ^2_y, and ρ_{xy}. This test was performed for each animal. $-2 \log \lambda$ is distributed as χ^2 with 2 degrees of freedom. The hypothesis was sustained by 22 of the 25 animals at the 0.05 level of confidence.

Test II. The hypothesis was that $\sigma^2_x=\sigma^2_y$ for the distribution of captures within an animal

where:

$$-2 \log_e \lambda = K_i \log_e \frac{(s_x+s_y)^2}{4s_x s_y} \qquad [14]$$

Assumptions: Same as in test I.
$-2 \log \lambda$ is distributed as χ^2 with 1 degree of freedom. The hypothesis was sustained by 24 of the 25 animals at the 0.05 level.

Test III. The hypothesis was that the coefficient of correlation, $\rho_{xy}=0$, for the distribution of captures within an animal

where:

$$-2 \log_e \lambda = K_i \log_e (1-r)^2 \qquad [15]$$

r is as defined in equation 13.

Assumptions: Same as in test I.
$-2 \log \lambda$ is distributed as χ^2 with 1 degree of freedom. The hypothesis was sustained by 23 of the 25 animals at the 0.05 level.

Test IV. The hypothesis was that all the (n) animals came from a population with the same variance (Bartlett's test for homogeneity of variances)

where:

$$-2 \log_e \lambda' = \left[\sum_{i=1}^{n} 2(K_i-1)\right] \log_e \frac{\sum_{i=1}^{n}\sum_{j=1}^{K_i} (x_{ij}^2+y_{ij}^2)}{\sum_{i=1}^{n} 2(K_i-1)} - \sum_{i=1}^{n} 2(K_i-1) \log_e \frac{\sum_{j=1}^{K_i} (x_{ij}^2+y_{ij}^2)}{2(K_i-1)} \qquad [16]$$

$$m = 1 + \frac{1}{3(n-1)} \left[\sum_{i=1}^{n} \frac{1}{2(K_i-1)} - \frac{1}{\sum_{i=1}^{n} 2(K_i-1)} \right] \qquad [17]$$

Assumption: $(x-\bar{x})$ and $(y-\bar{y})$ were independent and normally distributed with the same variance. $-2 \log \lambda'/m$, 72.59, is distributed as χ^2 with $n-1$ degrees of freedom. The hypothesis was rejected at the 0.001 level.

Test V. Hypothesis: Equation 4 as represented below by equation 22 approximates the frequency distribution of recapture radii from the mean coordinate center of the home range.

$$\text{Let } u_{ij} = \frac{x_{ij}-\bar{x}_i}{s_i} \text{ and } v_{ij} = \frac{y_{ij}-\bar{y}_i}{s_i} \qquad [18]$$

where ij represents the jth observation on the ith animal. That is, the variables u and v represent deviations from the respective means, i. e., centers of home ranges, for each animal expressed in standard deviation units. s_i^2 is the estimate of variance of an individual observation (radius) obtained by pooling the variance of x and y within each animal (see test II, which shows that $\sigma_x=\sigma_y$).

$$s_i^2 = \frac{\sum_{j=1}^{K_i} (x_{ij}-\bar{x}_i)^2 + \sum_{j=1}^{K_i} (y_{ij}-\bar{y}_i)^2}{2(K_i-1)} \qquad [19]$$

Of interest to investigators of this subject is the distribution of radii, that is, of

$$r_{ij} = (x_{ij}^2+y_{ij}^2)^{1/2} \qquad [20]$$

However, since the raw observations x and y have different variances (test IV) and different means among animals, it would be inappropriate to compare a radius, r_{ij}, of the ith animal with a radius r_{nj}, of the nth animal. Therefore, each radius was expressed in standard form denoted by Z_{ij}:

$$Z_{ij} = (u_{ij}^2+v_{ij}^2)^{1/2} \qquad [21]$$

This Z_{ij} was computed for each of the 348 observations and put into a frequency distribution with class intervals of size $0.3Z$. It was then desired to determine whether the theoretical frequency function

$$g(Z)dZ = Ze^{-Z/2}\,dZ \qquad [22]$$

that is, equation 4 with $Z=r/\sigma$, fitted the data. To this end, expected relative frequencies were computed by direct integration (table 3). Expected frequencies were then obtained (fig. 3), and a χ^2 goodness of fit test was made of these in comparison with the observed frequencies for 10 class intervals. The hypothesis that equation 22 was consistent with the data was sustained at the 0.5 level ($\chi^2=6.287$; 9 d. f.).

Equation 22 can also be derived mathematically from certain assumptions concerning the normal and independent distribution of x and y when it is assumed that the true means and standard deviations are known. For example, let μ_i, ν_i and σ_i be the respective means of x and y and the standard deviation for the ith animal. Then it is well known that $\frac{(x_{ij}-\mu_i)^2}{\sigma_i^2}$ and $\frac{(y_{ij}-\nu_i)^2}{\sigma_i^2}$ are each distributed like χ^2 with 1 degree of freedom. Hence their sum,

$$Z_{ij}^2=\frac{(x_{ij}-\mu_i)^2+(y_{ij}-\nu_i)^2}{\sigma_i^2} \qquad [23]$$

is distributed like a χ^2 with 2 degrees of freedom. Further Z_{ij}, is independent of Z_{il} and independent of Z_{nj}. Therefore, the distribution of Z_{ij}^2 is

$$f(Z^2)dZ^2=\tfrac{1}{2}e^{-Z^2/2}\,dZ^2 \qquad [24]$$

and it follows immediately that the distribution of Z is equation 22.

Successive Capture Derivation

Many persons have published data on the movement of animals as tabulations of the frequency of distances between successive captures. Such data provide a basis for obtaining a rough estimate of the group σ of the home range. For any two captures the mean coordinate point of capture, or calculated center of activity, lies halfway between the two observed points of capture. However, the true center of activity most probably lies to one side of the line connecting these points. Thus, the radial distance, r, of capture from the true center of activity is somewhat greater than half the distance between observed points of capture. The radial distance of capture from the calculated center of activity must be multiplied by $(n/n-1)^{1/2}$, where n is the number of captures for a given animal, in order to make the recapture radii, on the average, provide a more accurate estimate of the distance from the true center of activity. Where $n=2$, as in the case when distances, d, between successive captures only are considered, $r=0.5d\times1.414=0.707d$. When such procedures of calculation are followed, the home range σ, for practical purposes, should be approximated by that distance within which 0.394 of the r's fall. One note of caution: When the animal is caught at the same station on two successive dates, one must tabulate this simply as two r's of less than half the distance between traps forming the grid.

We wondered how the home range σ of male *Reithrodontomys* approximated in this way would compare with that of 52.7 feet estimated through the use of equation 8a. To this end, frequency tabulations were prepared of distances, d, between consecutive captures. Since the trapping stations were arranged in a 50-foot grid, only certain discrete d's were possible. This similarly limits the r's possible. These r's in feet followed by their frequency are: 0 (32); 35.4 (97); 50.2 (52); 70.7 (34); 79.1 (52); 100.4 (14); 106.0 (10); 111.8 (17); 127.2 (3); 141.2 (1); 145.9 (2); 150.1 (2); 158.1 (1); greater than 158.1 feet (2). The catch at each of these distances should represent the sampling of animals traveling within a band whose width extends halfway to the two contiguous radii. Thus, the widths of bands represented by the above r's vary from 4 to 25 feet.

If we knew the real home range σ, we could estimate the expected number of mice in each of these bands from figure 2. For this purpose, $\sigma=52.7$ feet as estimated independently by equation 8a, was used. These expected frequencies for the 14 r's were, respectively, 16.9, 72.5, 64.8, 46.9, 43.1, 29.3, 8.0, 13.4, 12.8, 3.8, 1.9, 1.6, 1.6, and 2.8. Although 3σ (158.1 feet) includes the correct number of r's as predicted by equation 7, there are some marked deviations between observed and expected frequencies. In particular, there are too many captures at the same station and at adjoining stations. Presumably this excess is due to the fact that Dr. Brant prebaited the traps part of the time and also occasionally left the traps at the four adjoining stations throughout several days of trapping. Thus any development of a trap-habit will produce too many short r's. Home range σ estimated as that distance including 0.394 of the captures is only 43.25 feet. Likewise, σ, when estimated as one-half the distance including 0.865 (from equation 6) of the captures, is 48.2 feet.

Another factor which may contribute to variation in the frequency distribution of r's is the fact that, from any one point of capture, 4 traps lie at some distances and 8 traps lie at others. This may well account for the relative excess of r's of 79.1 feet, for which there are 8 opportunities for capture, in contrast to the much fewer captures at 70.7 and 100.4 feet, for each of which there are only 4 such opportunities. Apparently, any estimation of σ from distances between consecutive captures is likely to be a much cruder one than that derived by the use of equation 8a or 8b.

Some criticism has been leveled at us by our mathematical and statistical colleagues for restricting our sample to 25 male harvest mice with only 348 captures. For example, 19 other males with 10 or more captures appeared either to have made a major shift in the center of their home range or only a small portion of their home range lay within the trapping plot, as indicated by the fact that captures of these mice were confined to the edge of the plot. These 19 males provided 216 d's for which derived r's ranged up to 496 feet. Home range σ estimated from those distances, including 0.395, 0.865, and 0.989 of the captures (equations 5–7) were, respectively, 45.6, 66.5, and 257.5 feet. If we include all 44 mice which had at least 10 captures, these three estimates of σ based upon 535 d's become 42.8, 56.1, and 229 feet.

Some recapture data, particularly those dependent upon short-term sampling, supply information primarily on the distance between two consecutive captures. This raises the question, "How can the best estimate of the home range sigma be derived from them?" A strict rule of thumb would be that $\sigma=(r_1+0.5r_2)/2$ where $r_1=0.707d$, which includes 0.394 of the captures, and $r_2=0.707d$, which includes 0.865 of the captures. However, one would be hard pressed to make a rigorous mathematical validation of this estimate. On a logical basis, the estimate minimizes the effect of the increased frequency of short r's arising from trap habit and from d's of those animals for which less than half of the home range is included in the sampling plot, and it also excludes the excessively long r's arising from shifts in the center of the home range. This extensive discussion of home range as reflected by distances between successive captures has been included in this section since it is apparent that persons involved in some of the more practical problems of wildlife management must rely on this sort of data for their estimate of the home range sigma.

General Considerations

From tests I to III, it may be concluded that for most of the mice the home range may be considered circular. However, the extent of home range varied significantly among the animals (test IV). Yet the pooled data of standardized radii (Z) was consistent with equation 22. If this is so, it follows that equation 4 probably describes the home range of any particular animal in terms of its own σ. Now, if equation 4 truly represents the probability of capturing an animal between radii r and $r+dr$ about the true center of home range, it follows that equations 2 and 3 probably represent a good approximation of the density function about the center of home range.

The parameter, σ, fixes all properties of equations 2, 3, and 4. To the extent that these equations depict home range, the following aspects of home range may be calculated:

- Idealized frequency of captures between any two radii.
- Density function at any radius.
- Probability of capturing an animal within any portion of its home range.

Such information may be derived from the data in tables 2 and 3 and from figures 1 and 2. In figure 1, the curve representing equation 2 is the cross section of the density function when $\sigma=1$. In order to convert this to any other σ, multiply the abscissa by σ and divide the ordinate by σ^2. The proportionate time an animal spends in any small portion of home range may be determined by multiplying the area by the density function at the radius of the center of the area. For example, the proportionate time an animal spends in a square 0.1σ on a side at radius σ is 0.00095 and at 2σ is 0.00021. The total amount of time spent in all areas within the $\pi(3\sigma)^2$ range is 0.9888.

Table 2 is a numerical tabulation of the curve in figure 1. To obtain the appropriate values,

Table 2. Normative data for calculating density function[1] in terms of area[2] for any value of σ

Radius (r) in σ units	Density function d (r)	Radius (r) in σ units	Density function d (r)
0. 0	0. 159	2. 1	0. 0176
. 3	. 152	2. 4	. 00886
. 6	. 133	2. 7	. 00415
. 9	. 106	3. 0	. 00175
1. 2	. 0776	3. 3	. 00068
1. 5	. 0517	3. 6	. 00024
1. 8	. 0315	3. 9	. 00008

[1] $\frac{1}{2\sigma^2\pi}e^{-r^2/2\sigma^2}$.

[2] Equation 1.

Table 3. Normative data for calculating expected captures for any value of σ

Class interval of radius of σ or Z	Expected proportion of total captures	Class interval of radius of σ or Z	Expected proportion of total captures
0. 0 –0. 3	0. 044	2. 101–2. 4	0. 054
. 301– . 6	. 121	2. 401–2. 7	. 030
. 601– . 9	. 168	2. 701–3. 0	. 015
. 901–1. 2	. 180	3. 001–3. 3	. 00674
1. 201–1. 5	. 162	3. 301–3. 6	. 00283
1. 501–1. 8	. 128	3. 601–3. 9	. 00104
1. 801–2. 1	. 087	3.901 and over	. 00049

the left hand column, the radius, must be multiplied by σ and the right hand column, the density function, must be divided by σ^2. By this procedure the density function is expressed in terms of the probability of capture per the square unit of distance in which σ is measured (feet, yards, etc.).

Since this curve (fig. 1) of density function represents the relative amount of time an animal spends per unit of area at various radii, it may represent the impact of the organism upon its environment. This curve may also be useful in calculating cohabitation. Cohabitation may be thought of in two ways. First, it may concern the total use of an area by all its inhabitants; this use will be proportional to the sum of the density functions. Second, it may concern the probability of simultaneous presence of individuals in the particular area concerned. This will be proportional to the product of their density functions at that place.

Figure 2 represents the integral of equation 4 and may be reconstructed from the data given in table 3. This curve is useful in calculating the probability of observing an animal up to or beyond a radius or between two radii. In order to convert this curve into values for any σ, multiply the abscissa by σ.

In figure 3 and table 3 the density function in terms of radius from center of home range assumes the shape of the theoretical or expected curve, which represents the probability of finding an animal within increments of radius

Figure 1. Cross section of the density function of home range in terms of area.

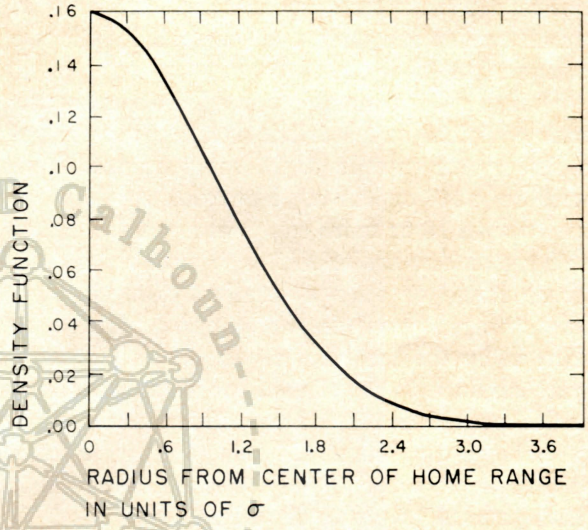


Figure 2. Accumulated probability of capture of mice in terms of radius from center of home range.

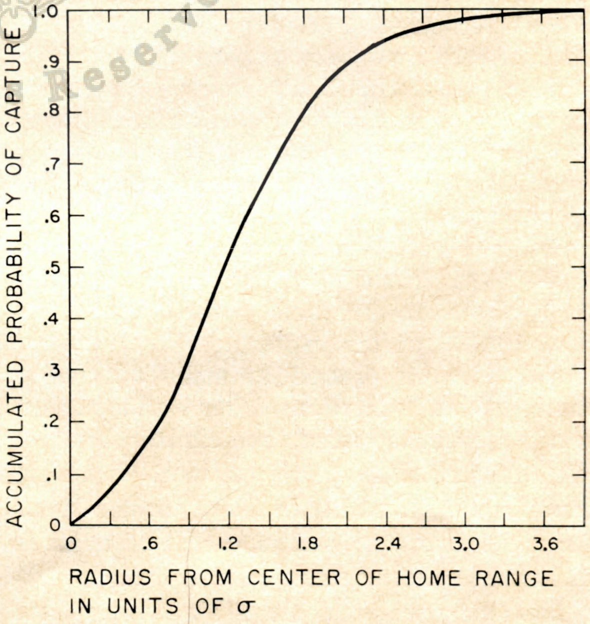
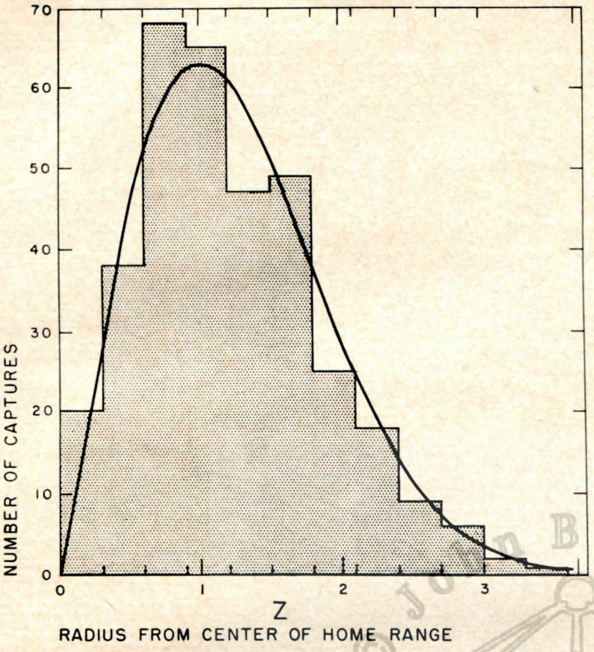


Figure 3. Observed (histogram) and theoretical distribution of 348 recapture radii (*Z*) of 25 male harvest mice from the center of their home range.



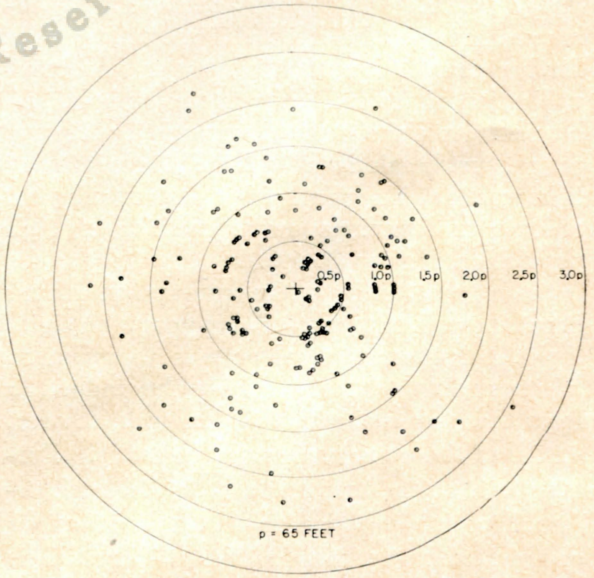
from the center of activity. Since the home range σ varied significantly among the 25 mice, each capture of each mouse was reexpressed in terms of its own σ by the Z transformation discussed in test V. The exact number of observed captures in the twelve 0.3 Z length class intervals shown are: 20, 38, 68, 65, 47, 49, 25, 18, 9, 6, 2, 1. In the chi square test the captures in the last three intervals were grouped together.

The method of collecting the present data was not ideal. In the first place, the traps were frequently prebaited for 6 days. Traps were occasionally left set at the same station for two or more consecutive days. Under such conditions an animal sometimes developed the habit of entering the same trap each consecutive day. We do not know how this biased the movement of the mice, other than to state that it is a common experience that prebaiting the traps increases the number of animals caught. A frequency plot was made of the recapture radii following prebaiting in contrast to those preceded by no prebaiting. These curves coincided so closely as to suggest that under the present conditions prebaiting had little if any effect in altering the behavior of male harvest mice. Ideally, what is desired is a large number of observations of each animal in the sample. Each such set of observations should cover a short span of time, probably 1 to 5 days for harvest mice, and the taking of observations should in no way disturb the animal or interfere with its movements. However, the home range of many mice was sufficiently stable that even when the observations were dispersed over a period of 2.5 to 8.0 months, there was no apparent change in the home range.

An appreciation of the general characteristics of home range may be secured by examining figure 4. Without any alteration in their orientation, each of the groups of captures for 25 mice were superimposed about a single center. The circles represent radial distances of proportions of p where $p=\sigma\sqrt{2}$, the radius encompassing 0.63 of the captures nearest the center. Traps were prebaited and left unset and untended for approximately 6 days. On the sixth day they were baited and set, and captures were recorded on the seventh day. Only captures taken under this regimen were used in the preparation of figure 4.

It is immediately apparent that the number of captures per unit of area decreases with distance from the center. It is also apparent that it would be possible for considerable overlap to develop in adjoining home ranges in the area of 1σ to 3σ from their centers without the inhabiting animals very frequently coming into

Figure 4. One hundred and ninety-four captures of 25 male harvest mice (*Reithrodontomys*) superimposed about a single center of home range.



contact or competing in their usage of the environment. This raises the question of the nature of the topography of the summated density functions for all individuals inhabiting an area.

We have not yet solved some of the technical problems inherent in integrating sums and products of density functions for all members of the population for every point in space. However, empirical calculations utilizing the data in table 2 lead to the following generalizations: When home range centers are characterized by an intervening distance greater than 2.0σ, the topography of summated density functions exhibits peaks and valleys. In other words, the environment is utilized most intensely near the centers of home range and least midway between centers. As home range centers become more uniformly distributed and as the interval between adjoining home range centers decreases, utilization of the environment becomes both more intense and more uniform. Nearly complete uniformity of usages is attained with an inter-home range center interval of 2.0σ distance. Any further decrease in the inter-home range center interval merely increases the intensity of usage of the environment without altering the uniform usage of the environment. Therefore, one might logically anticipate the evolutionary process to have culminated in behavior patterns assuring development of uniform distribution of home range centers having an inter-home range center interval of approximately 2.0σ. Where population density increases beyond this level and is accompanied by further contraction of home range size over-utilization of the environment must result. As a consequence the static characteristics of home range must break down and result in migratory behavior that is regularly observed among such rodents as lemmings during periods of high population density (*9, 10*).

Since, according to the concept presented here, there is actually no boundary or finite limits to home range, we propose to assign an arbitrary limit determined by the radius 3σ from the center of activity. In such an area, 0.9888 of the observations will be made. Furthermore, as the present data on *Reithrodontomys* show, it is practical to obtain observations of home range up to this limit at least. This method of describing the home range should provide figures similar to those obtained with the "minimum area" method commonly used by mammalogists, in which an area is determined by the polygon encompassing the outermost points of observation. At least, this similarity in representation should result if no shift in centers of activity occurred in the period during which the "minimum area" was determined. If a shift in the center of activity takes place, an overestimate of the size of the home range would result.

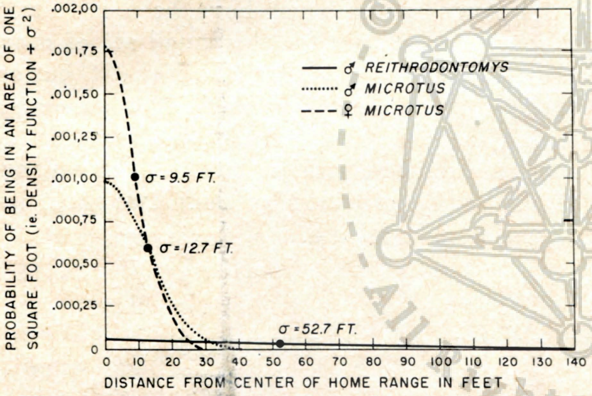
Such a comparison may be made by utilizing the data presented by Hayne for *Microtus*, for which a 60-foot spacing interval of traps was used (*4, 5*). The average estimate for individuals with three or more captures was 0.194 acre for females and 0.429 acre for males. The σ values were calculated from table 1 of Hayne's data (*4*) for males, after excluding all animals caught at only one trapping station. This gave a σ of 9.5 feet for females, with a 3σ circular area of 0.059 acre, and a σ of 12.7 feet for males, with a 3σ circular area of 0.104 acre.

In these calculations approximately 12 percent of the observations for each sex fell beyond 3σ. This suggests that about 10 percent of the observations represented cases in which shifts in the center of activity had occurred. It was undoubtedly the inclusion of these 10 percent of the observations in Hayne's calculations which produced the markedly greater estimate of the area of the home range by the use of his "minimum area" method. For this reason, we believe that the method of determining the area of the home range presented in this paper is a more realistic one for estimating the actual area used.

Furthermore, the intensity of usage of different portions of the home range may be demonstrated by calculating the density function in terms of area. Such a comparison of density function was made for both male and female *Microtus*, as well as for male *Reithrodontomys*, by utilizing the above values of σ, calculated from Hayne's data. These values are shown in figure 5, which indicates that small differences in the home range parameter, σ, produce much greater differences in the probability of observing the animals per unit of area.

Although the curves in figure 5 represent the relative amount of time the animal spends per unit of area from the center of the home range, a certain amount of caution needs to be exercised in utilizing this density function as an index of the relative impact of an organism upon its environment. First, different behaviors, such as those involved in securing nesting material or food or in the investigation of the environment, may each have their own density function. Second, when comparing two different species, density function cannot be utilized for equating their impact upon the environment unless both species are similar in all their properties. For example, a mouse and a deer might exhibit the same density function curve but, because of differences in size and behavior, the impact of each species upon the environment would be different, both qualitatively and quantitatively.

Figure 5. Comparative probabilities of being in an area of 1 square foot for three groups of mice.



There is still much to be learned regarding the density function of different behaviors occurring within the home range. Several other questions are also much in need of clarification:

- To what extent does the calculated center of the home range actually represent one or more major goals, such as a place of harborage or source of water, about which the individual animal orients its other activities?

- What is the character of the paths of locomotion from and toward the center of activity? Are the outward and return trips identical in duration and in the types of activities exhibited during them?

- How does the structure of the environment affect the density function? That it must affect it is shown by the data presented by Stickel (*11*) for deer mice (*Peromyscus*) inhabiting bottomland and upland forests. The mice in the latter habitat regularly exhibited larger home ranges than did those inhabiting the bottomland. Both the quantity of a goal per unit of area and the distance separating goals should be important variables. Blair presents similar data for *Microtus* (*12*).

- How does social behavior alter the density function of the home range? Where there is no territorial behavior and the environment is uniform, the number of centers of the home range of individual animals or colonies per unit of area should be distributed at random, that is, a Poisson distribution. As territorial behavior approaches a maximum, one would expect the nearest approximation to a uniform distribution of centers of activity, that is, there would be a minimum variance in the distance between centers of adjoining home ranges. Clark and Evans have presented a method of analyzing this question (*13*).

There is much in the literature which permits one to voice opinions about some of these problems. However, not until they are investigated systematically and quantitatively will it be possible to develop an understanding of the ecology of home range. Such an understanding has considerable relevance to the problem of population density.

More effective utilization of space is a basic problem in human sociology, animal husbandry, and wildlife management. In each of these areas, the circumstances of the present age exert increasing pressure for greater population densities. The approach toward greater densities involves three processes:

- Development of a smaller home range σ.

- Simultaneous coexistence of more individuals within the same home range.

- A more uniform distribution of centers of home range.

However, although the development of a science of home range will assist in producing desired densities, it is well to bear in mind that determination of numbers of animals is only one of several goals. Biomass of the community, growth of the individual, the social stability of the group, and the psychological well-being of the individual are other goals

(*14*), and the degree of attainment of any one of these goals necessarily modifies the degree of attainment of the others. Home range may thus be seen to form an important concept in equating these goals in relation to whatever value system we wish to impose upon them.

Dice and Clark (*15*) have presented a treatment of home range which closely parallels ours in its approach to the problem. Their data included 32 deer mice, *Peromyscus*, which were captured on an average of 5.5 times each. Males, females, adults, and juveniles were included in the sample. Each recapture radius from the calculated center of activity was subjected to a square root transformation and the resultant data were tested for conformity to a Pearson's type III probability function. With 15 class intervals of recapture radii there resulted a chi square of 20.08, which indicates significant heterogeneity from that hypothesized.

We subjected the data of Dice and Clark to a test for conformity with the bivariate normal distribution of home range which we have proposed. The standard deviation was approximated as that radius, 65 feet, within which 0.394 of the captures fell (equation 5). The numbers of captures in the 10 class intervals (table 3) from 0 to 3σ were, respectively: 6, 28, 28, 34, 18, 20, 25, 6, 7, and 2, while beyond 3σ there were 9 captures. Chi square was 40.4, with 24.5 of this contributed by captures beyond 3σ. Considering the fact that the small number of captures per individual precluded determination of possible shifts in center of home range, and that animals with different-sized home ranges must have been included, it is concluded that for this small set of data no equations can be found which fit better than do Dice's and Clark's (*15*) or ours and that either at least roughly describes home range as exhibited by these data. A comparison of the results provided by these two methods is presented in table 4.

Table 4. Home range of *Peromyscus*

Accumulated probability of capture	Radial distance (feet)		
	Observed	Calculated by method of—	
		Dice and Clark [1]	Calhoun and Casby [2]
0. 25	46	50	52
. 50	77	79	77
. 75	116	118	109
. 95	185	193	161
. 99	255	260	214

[1] Reference 15.

[2] Public Health Monograph No. 55, figure 2

North American Census of Small Mammals

A number of mammalogists have cooperated in the utilization of a standardized procedure which provides data on relative densities of such genera as the mice *Peromyscus*, *Clethrionomys*, *Microtus*, *Reithrodontomys*, and *Sigmodon*, as well as the shrews *Blarina* and *Sorex* (*2*). This procedure consists of placing three traps within a radius of 2.5 to 5.0 feet from a station marker. Traps are left set for 3 consecutive days. The animals are killed and removed each day. A straight line of 20 stations forms the basic sampling unit. An interval of 50 feet between stations is customarily used. A summary of results from 744 traplines run from 1948 through 1951 is given in table 5.

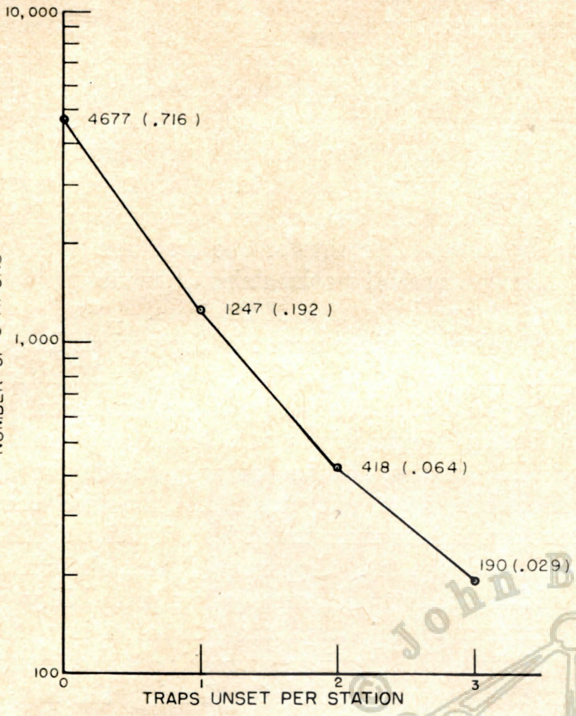
The concept behind placing three traps at each station was that, even after one or more animals had been caught, there would still be a set trap available for capturing another indi-

Table 5. Total captures on 744 North American Census of Small Mammals traplines [1]

Day	Number of stations capturing—			
	0 animals	1 animal	2 animals	3 animals
1	12, 244	2, 030	483	123
2	12, 839	1, 692	284	65
3	13, 243	1, 368	223	46

[1] Each trapline consisted of 20 stations with 3 traps per station. On 77 percent of the lines, the interval between stations was 50 feet; on the remainder, 25 feet.

Figure 6. Functional efficiency of trapping stations.



vidual. As soon as three mice had been caught at a station during a day, any others which approached the traps would be turned away. When all traps functioned perfectly, only a small number of stations (0.0052 of total) had the opportunity of turning mice away (table 5). Actually, a somewhat larger number of stations turned mice away because some traps were sprung accidentally. Data were available from a portion of the traplines showing the number of traps unset at each station each day (fig. 6). Based upon this sample of the number of traps found unset within a 24-hour period, it is apparent that the efficiency of the trapping stations was not unduly lowered by traps becoming unset by wind, rain, larger animals, and so on. Assuming that the data in table 5 are representative, the sampling device has a high operational efficiency.

An approximation of the number of animals which may be turned away by unset traps on the first day of trapping may be made (table 6) by taking into consideration the data in figure 6 along with that in table 6 which concerns the number of stations catching 0, 1, 2, or 3 animals. These are probably slight underestimates.

Figure 7. Accumulated captures of mice along all North American Census of Small Mammals traplines from end of trapline to center, 1948–51.

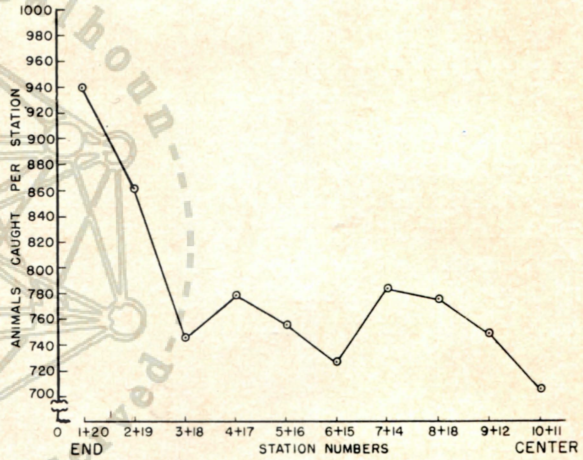
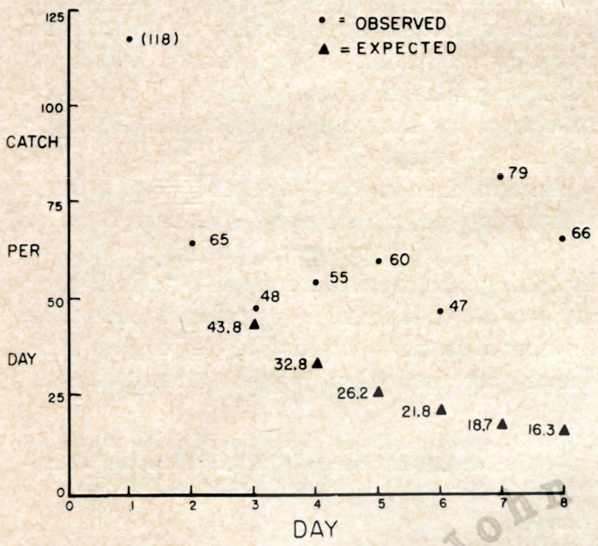


Table 6. Trapline data from North American Census of Small Mammals, 1948–51

Total 3-day catch (range)	Number of trap-lines	Mean daily catch			Three-day total (mean)	Number stations with catch on day 1 of—				Approximate proportion of approaching animals turned away on day 1
		Day 1	Day 2	Day 3		0	1	2	3	
Total	845	4. 25	3. 22	2. 45	9. 92	14, 083	2, 190	502	125	----------
0–9	575	1. 7	1. 3	0. 9	3. 9	10,609	827	60	4	0. 033
10–19	166	6. 1	4. 2	3. 2	13. 5	2,460	726	120	14	. 040
20–29	55	10. 6	7. 2	5. 9	23. 7	648	335	104	13	. 047
30–39	18	13. 9	11. 3	8. 9	34. 1	181	115	57	7	. 050
40–59	15	18. 1	14. 6	11. 3	44. 0	129	95	51	25	. 073
50 and over	16	31. 1	22. 6	22. 1	75. 8	56	92	110	62	. 150

Figure 8. Observed and expected catch of small mammals taken during 8 consecutive days of trapping along 12 North American Census of Small Mammals traplines.



However, it is apparent that when the total 3-day catch on a trapline exceeds 35 animals, not more than 95 percent of the animals approaching the trap on day 1 are caught. When the anticipated catch for 3 days exceeds 35 animals per trapline, 4 or more traps per station are needed.

Only rarely is it necessary to take the precaution of providing additional traps since the 3-day catch for a trapline will exceed 35 animals only 5 percent of the time (table 6). Each successive day the catch will decline. There is no systematic difference in the rate of decline in the daily catch within the range of 4 to 44 animals per trapline for 3 days.

In this study, the largest number of animals was captured on the two terminal stations, Nos. 1 and 20 (fig. 7). A smaller number were taken on stations Nos. 2 and 19, which are adjacent to the terminal ones. The other 16 internal stations had approximately equivalent catches but less than the 4 stations at or next to the end of the trapline, indicating that a 50-foot interval between stations is too short to prevent competition between adjacent stations for the available animals. The 16 centrally located trapline stations primarily drew victims only from either side of the trapline, whereas the two terminal stations also drew victims who lived beyond the ends of the lines.

Twelve traplines were run for periods longer than the usual 3 days (*16*). One would anticipate that continued trapping and removal of the animal population would lead to a continued decline in the number of animals caught on successive days, but such is not the case when the trapline is surrounded by extensive similar habitat (fig. 8). Apparently animals which initially have an extremely low probability of exposure to the traps are attracted into the vicinity of the trapline as a result of the removal of the previous residents. During the last 6 days of trapping, the total observed catch was over twice that of the expected total for this period. This increase in the observed catch presumably was caused by invasion by animals from surrounding areas, and by expansion of home range by certain subordinate members of the community. Full documentation of the latter concept will be presented in another publication at a later date. The expected catch per day was calculated by using equation 54.

The preceding paragraphs describe a widely used procedure for sampling populations of small mammals. We shall now proceed to show how the captures on days 1 and 2 in conjunction with data on home range can be used to estimate density.

Estimation of Population Density

The data from the North American Census of Small Mammals were derived from a sequence of daily samples from the animal population. Several persons have estimated density from such a sequence of samples (*17–21*). Throughout these papers there is a common rationale, which we have paraphrased as follows:

Initial population$=N$

Proportion of remaining animals captured per night$=P$

First night's capture, $C_1=NP$ [25]

Residual population after first night, $N-NP=N(1-P)$ [26]

Second night's capture, $C_2=PN(1-P)$ [27]

Residual population after second night, $N(1-P)-PN(1-P)=N(1-P)^2$ [28]

By extension:

Capture on *n*th night, $C_n=PN(1-P)^{n-1}$ [29]

Residual population after $(n-1)^{st}$ night $=N(1-P)^{n-1}$ [30]

Therefore, total capture up to but not including *n*th night, T_n

$$=N-N(1-P)^{n-1} \quad [31]$$

$$=N[1-(1-P)^{n-1}] \quad [32]$$

Both C_n and T_n contain the common parameter, $(1-P)^{n-1}$. We eliminate the parameter by substitution.

$$T_n=N\left(1-\frac{C_n}{PN}\right) \quad [33]$$

$$C_n=P(N-T_n) \quad [34]$$

This is the equation of a straight line (fig. 9), as proposed by Hayne (*19*). Our equation 29 is essentially that presented by Moran (*20*), and our equation 33 is essentially that presented by Leslie and Davis (*17*), DeLury (*18*), and Hayne (*19*). Hayne's method is applicable only to those conditions in which all animals have the same probability of capture by the sampling devices. Our equations 34 and 35 are applicable to this curve.

From equations 25 and 27:

$$N=\frac{C_1}{1-C_2/C_1} \quad [35]$$

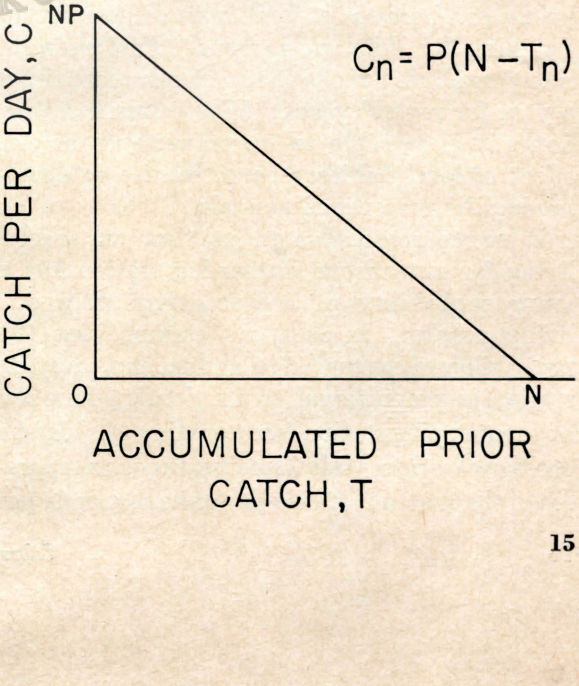
The questions we posed initially were: Are equations 33 and 34 applicable to the data secured by the North American Census of Small Mammals? Equation 33 applies only to the population in an enclosed area in which at the beginning of each sampling period each animal has the same probability of capture.

Moran (*20*) was cognizant of this limitation to the use of equation 33, for he says: "The last and perhaps the most important reservation about the above theory is that it assumes that the chance of being trapped is the same for each animal." Zippin (*21*) accepts the logic propounded by Moran, Leslie and Davis, DeLury, and Hayne, with its recognition that such procedures for estimating density are valid only if "the probability of capture during a trapping is the same for all animals."

The following combinations of sampling procedures and characteristics of movement by members of the animal population represent the major conditions giving rise to a constant probability of capture:

A. If there are sufficient sampling devices in

Figure 9. Graphic method of calculating density of mice (*N*) according to Hayne.



the area to insure that all areas are equally depleted, equation 33 applies.

B. If each animal moves at random through the area, equation 33 applies regardless of the pattern in which the devices are set, as long as no animals are rejected for want of opportunity of entering devices already full.

C. If the sampling devices are placed each day without regard to the position they held the previous day, equation 33 applies, regardless of whether the individuals move at random or have some stationary statistics such as in equation 2.

The sampling procedure utilized by the North American Census of Small Mammals and the characteristics of movement of the animals studied are such as rarely to satisfy any of these conditions. The "A" conditions are violated because traplines are customarily placed in environments so extensive that many animals have a very low probability of encountering traps because they live at such long distances from the traplines. In other words, for practical purposes we are not dealing with enclosed areas. The "B" conditions are violated by the fact that small mammals do not move through the habitat at random but rather have a home range similar to that represented by equation 2. The "C" conditions are violated by the fact that the traps were left in the same position on successive days. Thus, it is apparent that equation 33 will not serve satisfactorily in estimating density from the day-to-day removal catches obtained by the North American Census of Small Mammals.

The procedure of fixed trapping stations has been used because it facilitates conformity of sampling by different persons. Furthermore, many traplines have been run two or more times a year for several years. Where this has been done, it is possible to make analyses of the effect of local habitat characteristics in determining the presence of animals.

It seems reasonable to us that an animal living far away from a trapping station has a lower probability of capture than does one living nearby. In fact, we assume that the probability of capture of an animal at a trapping station is proportional to its density function at the trapping station (see equation 3). In the ecological sense, this density function represents the amount of time an animal spends per unit of area within its home range. Where the sampling device remains at the same position throughout the taking of the several consecutive samples, and where, for practical purposes, the habitat about the sampling device is infinite with reference to the animal's daily movements, the probability of capture requires further consideration.

If, as we believe, the hazard area about a trapping station is relatively small, the number of times an animal encounters a station will be proportional to the density function of the animal at the station. In the vicinity of any one trapping station located so as not to be in competition with any other station, there will be distributed animals whose centers of home range lie at varying distances from the trapping station. Therefore, each of these animals will have a particular expectation of capture dependent upon the distance of the center of its home range from the trapping station. The expectation of capture $(E(W))$* is used in the sense of the percentage of nights an animal would be captured in a trap provided it were released each morning and no learning by the animal were involved.

Suppose a trap is situated in an animal's home range at the coordinate (x', y'), which is at distance $(x'^2+y'^2)^{1/2}=W$ from the center. The density function expressing the probability of the animal being at this point (x', y') is either

$$\frac{1}{2\pi\sigma^2} e^{-(x'^2+y'^2)/2\sigma^2} dx'dy' \qquad [36]$$

or

$$\frac{1}{2\pi\sigma^2} e^{-W^2/2\sigma^2} dx'dy' \qquad [37]$$

The expectation of capture of this particular animal will be proportional to the density of the species at that coordinate and will be

$$\frac{K}{2\pi\sigma^2} e^{-W^2/2\sigma^2} = E(W) \qquad [38]$$

Since a priori there is an equal likelihood of a center of home range occurring at any point in the environment, it follows that the number

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*Our use of the word "expectation" and the symbol $E(W)$ do not exactly correspond with the customary use of these terms in statistics and probability. In the latter sense $E(W) = \int W f(W) dW$. Here, $E(W)$ more closely corresponds to a binomial expectation in that it represents the relative frequency of captures.

of animals, $N(W)$, whose centers of home range fall within a ring about the trapping station of radius W and width dW is

$$N(W)=c2\pi WdW \tag{39}$$

where c is number of animals per unit area.

Then the expected capture of animals from the ring will be the product of equations 38 and 39:

$$\frac{K}{2\pi\sigma^2}e^{-W^2/2\sigma^2}2\pi cWdW \tag{40}$$

Finally, the expected capture on day 1, C_1, from all territory surrounding the trapping station will be the integral of equation 40.

$$\int_0^\infty \frac{K}{2\pi\sigma^2}e^{-W^2/2\sigma^2}2\pi cWdW \tag{41}$$

The expected residual population in the ring at W after removing the captures on the first night will be

$$N(W)dW-N(W)E(W)dW =N(W)[1-E(W)]dW \tag{42}$$

and the expected capture on the second night will be

$$C_2=\int_0^\infty E(W)N(W)[1-E(W)]dW \tag{43}$$

and, in general, the expected capture on the nth night will be

$$C_n=\int_0^\infty E(W)N(W)[1-E(W)]^{n-1}dW \tag{44}$$

It follows that

$$C_n=\frac{\pi c2\sigma^2}{n}\left[1-\left(1-\frac{K}{2\pi\sigma^2}\right)^n\right] \tag{45}$$

The above equations may be simplified so as to solve for c, the animals per unit of area: Expected captures on day 1:

$$C_1=\pi c2\sigma^2\left(\frac{K}{\pi 2\sigma^2}\right) \tag{46}$$

Expected captures on day 2:

$$C_2=\frac{\pi c2\sigma^2}{2}\left[1-\left(1-\frac{K}{\pi 2\sigma^2}\right)^2\right] \tag{47}$$

Expected captures on day 3:

$$C_3=\frac{\pi c2\sigma^2}{3}\left[1-\left(1-\frac{K}{\pi 2\sigma^2}\right)^3\right] \tag{48}$$

The functions $\pi c2\sigma^2$ and $\frac{K}{\pi 2\sigma^2}$ occur as parameters of these equations. It will be helpful in interpreting these equations if we can gain more insight into the meaning of these two functions.

Since c represents the animals per unit of area and σ^2 represents the range of each animal in units of area, $c\sigma^2$ is an expression of the intensity of occupancy in terms of the static characteristics of extent of home range. In other words, $c\sigma^2$ denotes the extent of overlap of home ranges and the scarcity of space unoccupied by animals. K represents a kind of velocity with which an animal covers its home range and $\frac{K}{\pi 2\sigma^2}$ the frequency with which it visits a particular place. The latter we designate as the visitation frequency. This parameter is essentially that treated in military observation problems, such as detection of submarines from airplanes during World War II (*22*).

Thus, each day's catch is compounded of the intensity of occupancy function, $c\sigma^2$ and the visitation frequency, $\frac{K}{\pi 2\sigma^2}$. However, the ratio, C_2/C_1 depends entirely upon the visitation frequency:

$$C_2/C_1=1-\frac{K}{2\pi 2\sigma^2} \tag{49}$$

Therefore

$$\frac{K}{\pi 2\sigma^2}=2[1-C_2/C_1] \tag{50}$$

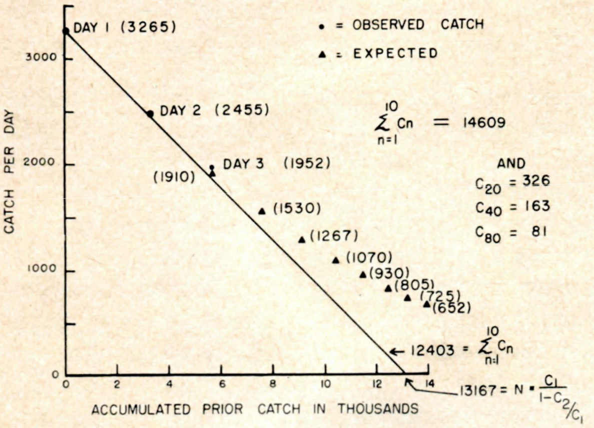
and so, if σ is known, c (animals per unit of area) can be calculated using equation 46.

$$c=\frac{C_1}{4\pi\sigma^2(1-C_2/C_1)} \tag{51}$$

where C_1 and C_2 represent the captures per trapping station on nights 1 and 2.

In handling actual sets of data, there arises the problem of predicting what the actual catch would be provided sampling were continued without any change in the activities of the animals remaining within an area.

Figure 10. Comparison of observed and expected daily catches of mice along 744 North American Census of Small Mammals traplines during 1948–51, based on two hypotheses.



$$\text{Let } U = \frac{K}{\pi 2\sigma^2} \qquad [52]$$

$$= 2(1 - C_2/C_1)^* \qquad [53]$$

and, then from equations 45 and 46

$$C_n = \frac{C_1}{nU}[1-(1-U)^n] \qquad [54]$$

By calculating U from the catches on the first 2 days of trapping and inserting this quantity in equation 54, the predicted catch on any following day may be estimated. Because of variability in C_1 and C_2 resulting from chance and vagaries of the weather, several sets of such data are needed for use of equation 54.

The observed catch for 3 days and the expected numbers of mice caught through a longer sequence of time are shown in figure 10. The expected numbers indicated by the straight line are derived from equation 35, which assumes a constant probability of capturing all animals. This hypothesis produces a lower calculated catch than the expected numbers derived from equation 54, shown as triangles in figure 10. This latter hypothesis assumes that animals living farther from the trapping station have lower probabilities of capture.

From equation 38, U represents the expectation of capture of a particular animal whose center of home range is at 0 distance from the trapping station; therefore, U must be between 0 and 1. If this is so, then from equation 53, C_2/C_1 must be between 0.5 and 1. Similarly, C_3/C_2 must lie between 2/3 and 1; C_4/C_3 between 3/4 and 1, and so on to C_{n+1}/C_n between $n/\text{n}+1$ and 1.

As shown in test IV in the section, "Derivation of Home Range," σ varies significantly among animals, and in equation 38 we were forced to use a grouped σ (s as in equation 8a). Determination of the distribution of σ requires more data than is now at hand. However, if this distribution were known, equation 38 could be replaced by

$$E(W) = \int_0^\infty \left[\frac{K}{\pi 2\sigma^2} e^{-W^2/2\sigma^2}\right] f(\sigma^2)\, d\sigma^2 \qquad [55]$$

Then equations 39 to 51 would be correspondingly altered toward greater accuracy in estimating density. Likewise, the reliability of estimates of density requires a knowledge of the distribution of C_2/C_1 where C_2 is not independent of C_1. For the purposes of our formulations we have considered small mammals as a biological entity. Further use of these formulations demands that restrictions of species, sex, habitat, and perhaps season be placed on C_2/C_1 as well as the home range σ.

In the preceding formulations we were concerned primarily with the development of means of estimating density from removal trapping such as is represented by the procedure utilized in the North American Census of Small Mammals. This effort culminated in equation 51, which utilized only data for captures on the first 2 days of trapping since continued removal thereafter is usually accompanied by invasion by animals from other areas or by expansion of home range of survivors (fig. 5).

However, it is theoretically possible to obtain data on density of animals without altering patterns of movement. Were all animals marked for visual identification, the number of individuals appearing at a particular point for the first time on each successive day could be recorded, when capture-mark-release-and-recapture procedures are used, the number of unmarked animals entering traps each day can be recorded. However, two precautions must be exercised. First, there must be enough live traps at each station to capture every animal which approaches a trap. Second, stations

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*See equation 50.

must be far enough apart so as not to compete for the opportunity of capturing animals living between stations. For rodents such as *Clethrionomys*, *Peromyscus*, *Reithrodontomys*, and *Sigmodon*, which generally appear to form, at most, family groups or other small aggregates, there should be at least 5 traps at each station, and stations should be located at least 4 to 6 home range σ apart. For example, stations should be 60 to 80 feet apart for *Microtus* and 240 to 360 feet apart for *Peromyscus*. We are aware of no live-trapping data which fulfill these requirements.

Where the procedures of sampling do not disrupt the stationary statistics of home range, i. e., invasion and alteration of σ, a further estimate of density, c, follows from equation 45.

In such situations, when it is reasonable to assume that c and K remain constant for captures on all n days, it should be pointed out that these parameters can be estimated directly by utilizing all captures on all n days, rather than from the first and second night captures only. Equation 45, which contains the parameters nonlinearly, can be differenced so that the logarithm of the differences in captures on successive nights is linear in c and K.

The steps are as follows:

From equation 45

$$nC_n=2\pi\sigma^2c\left[1-\left(1-\frac{K}{2\pi\sigma^2}\right)^n\right] \qquad [56]$$

Therefore

$$(n-1)C_{n-1}=2\pi\sigma^2c\left[1-\left(1-\frac{K}{2\pi\sigma^2}\right)^{n-1}\right] \qquad [57]$$

Thus

$$\begin{aligned}\Delta(n-1)C_{n-1}&=nC_n-[(n-1)C_{n-1}]\\&=2\pi\sigma^2c\left(1-\frac{K}{2\pi\sigma^2}\right)^{n-1}\left[1-\left(1-\frac{K}{2\pi\sigma^2}\right)\right]\\&=cK\left(1-\frac{K}{2\pi\sigma^2}\right)^{n-1} \qquad [58]\end{aligned}$$

Therefore

$$\log\Delta(n-1)C_{n-1}=\log cK+(n-1)\log\left(1-\frac{K}{2\pi\sigma^2}\right) \qquad [59]$$

Now plotting the logarithm of $[nC_n-(n-1)C_{n-1}]$ against $n-1$ should result in a straight line whose intercept and slope can be estimated by least squares or graphically. In practice, in order to avoid negative differences of $[nC_n-(n-1)C_{n-1}]$, it may be necessary to fit a smoothed curve through the capture data. Then each C_n and its C_{n-1} would be read from the smoothed curve. The intercept of course is equal to log cK and the slope is equal to log $\left(1-\frac{K}{2\pi\sigma^2}\right)$. Taking antilogs, we find cK and $\frac{K}{2\pi\sigma^2}$ and hence for known σ^2, c and K may be calculated. For example, if the intercept and slope are denoted by a and b respectively, we have

$$\log cK=a \qquad [60]$$

and

$$\log\left(1-\frac{K}{2\pi\sigma^2}\right)=b \qquad [61]$$

From equation 61

$$\hat{K}=2\pi\sigma^2(1-\text{antilog } b) \qquad [62]$$

and substituting in equation 60

$$\hat{c}=\frac{\text{antilog } a}{2\pi\sigma^2(1-\text{antilog } b)} \qquad [63]$$

Determination of density by equation 63 has the advantage in that it is applicable to a single consecutive series of samplings, whereas equation 51 demands several sets of data on C_1 and C_2 in order to cancel variability caused by weather conditions which modify the activity of the animals.

In the text directly following equation 48 brief mention was made of what we understand K to represent. Now that it is possible to estimate K, further comment concerning what is subsumed under it is justified. K is a kind of velocity in that it probably includes:

- Actual rate of travel.
- The perception swath the animal "cuts" through its environment. If an animal can detect a trap or similar stimulus 10 feet away, it will cut a 20-foot perception swath along its route of travel. Thus, where all other factors are equal, an animal cutting a 20-foot perception swath will be more likely to be captured than one cutting only a 10-foot swath.
- The number of trips per unit of time away from home and back again.
- The pattern of movement. An animal which retraces homeward the same route it

Table 7. Captures of male *Reithrodontomys* from the North American Census of Small Mammals census tract California 1—I and II [1]

Day	Number of stations with catches of—				Total catch
	0	1	2	3	
Total	348	117	13	2	149
1	99	53	7	1	70
2	123	33	4	0	41
3	126	31	2	1	38

[1] Run by Dr. Brant 4 times during 1950 and 1951. This was the tract from which the home range parameter, σ, of 52.7 feet was determined. (See equation 8a.)

traveled outward will be less likely to encounter any particular point than one which moves outward radially, traverses an arc, and then returns homeward along a different radius.

K might will be more appropriately designated as a scanning constant. It is presented as a necessary postulate to understanding home range dynamics. All four variables which contribute to it may be measured on a practical basis.

Table 7 presents the kind of data requisite to calculating population density. Since in the 8 traplines there were 160 trapping stations, each run 3 nights, the mean catch per trapping station on day 1 was 0.437, 70/160; and

$$C_2/C_1=0.585;\ \text{and}\ \sigma=52.7\ \text{feet} \qquad [64]$$

Therefore, from equation 51

$$c=0.437/4\pi(52.7)^2(1-0.585) \qquad [65]$$

$$=0.0000302\ \text{male}\ \textit{Reithrodontomys}\ \text{per square foot, or 1.316 per acre.}$$

In the censuses run by Dr. Brant (*6*) there were also female *Reithrodontomys*, as well as male and female *Peromyscus* and *Microtus*. The total catches for the 8 traplines in this sample were 43, 29, 85, 63, 78, 70, 49, 19. Thus, in addition to the 149 male *Reithrodontomys*, 287 other animals entered the traps. Some animals must have been turned away because all three traps at a station were full.

This turning away of animals may have produced a slight error in the calculation of the population density of male *Reithrodontomys*. It again emphasizes the necessity of having a sufficient number of traps per trapping station so that no animal will be turned away (tables 6 and 7).

Sampling Populations of Small Mammals

Adequacy of Sampling Device

Whenever animals are turned away from a sampling station because of the inadequacy of the sampling device, too small a C_1 will result. The animals turned away will be likely to augment C_2, C_3, and so on. C_2/C_1 will be too large, and an overestimate of density will result. The preceding example of the calculation of density of *Reithrodontomys* certainly involved such an error.

Hine's data* illustrate the aberrations which may result from an inadequate sampling device. She ran 103 traplines for 3 consecutive days. Several localities were represented, and each was sampled during several months of the year. Thus, any favoring of an increased catch on any one of the 3 days because of weather was probably cancelled. Each trapline consisted of 50 traps placed in a line, with 1 trap per station and with 100 feet between stations. On each of the first, second, and third days of trapping, 5,150 stations were represented, for which the total daily catches of 1 animal per station were 519, 546, and 495, respectively, for each of the 3 days.

Considering the large size of these samples, and that all animals were killed and removed from the traps each day, the fact that the catch for each consecutive day did not decrease presents an apparent anomaly. However, since the animal population sampled consisted of

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*See Acknowledgments.

small mammals, such as *Peromyscus*, *Blarina*, and *Microtus*, as was also true of the populations for which data are presented in the North American Census of Small Mammals, there was every reason to believe that 2 and sometimes 3 animals did arrive at many of the stations during a single day. When this happened, the extra 1 or 2 individuals must have been turned away from these single-trap trapping stations.

If the animals which are turned away from the trapping stations keep returning to the newfound source of food until they find a trap unoccupied, one may anticipate a series of catches over the 3 days much like the catches found by Dr. Hine. In fact, by taking the data in table 5 for known numbers of second and third captures and assuming that the population was, instead, sampled by only one trap per station, and furthermore, that the animals turned away kept coming back to the same station until they found a trap empty, one will derive catches C_1, C_2, and C_3, which are very similar percentagewise to those of Dr. Hine.

Variations in Size of Daily Catch

Both random sampling error and temporal changes in the weather produce variations in C_1 and C_2. We have not as yet attempted to estimate how many determinations of C_1 and C_2 are required for adequate averaging of such variations. Until the effect of fluctuations in weather on this variation is known, precaution must be taken to include several pairs of different days when using equation 51. The following is an excellent example of how weather may occasionally modify the relationship between C_1 and C_2.

Only infrequently is C_2 greater than C_1. Yet William L. Webb reported that each of eight North American Census of Small Mammals traplines set out on October 10, 1951, had greater catches on the second day of trapping than on the first day (*2*). Totals were: C_1, 19; and C_2, 52. Eight other lines, 4 set out September 4, and 4 set out September 10, in a neighboring habitat all gave the usual higher C_1. Totals were: C_1, 116; and C_2, 67. Although the weather changes on these dates are not definitely known, it is unlikely that the greater C_2's on the lines set out October 10 were due to chance error.

Invasion

The problem of invasion has already been mentioned in the description of the North American Census of Small Mammals. The numbers of animals taken in and removed from traps on days 3 through 8 (fig. 8) were considerably larger than the numbers anticipated by the use of equation 54. Verification of the validity of equation 54 probably cannot be accomplished by procedures which kill the animals captured by the sampling device, because invasion results. Testing the accuracy of equation 54 probably can be accomplished only by marking and releasing the animals. The sequence of captures of unmarked individuals is the one to compare with this equation. It is probable that even C_1 and C_2 are slightly increased by invasion when kill-trapping is employed.

Competition Between Sampling Stations

In areas where stations are too close together the mean number of captures per station will be reduced (fig. 7) since some animals which would be taken by a particular station are instead removed by neighboring ones. When using equation 51, this leads to an underestimate of density. Where home range has been determined, and stations are placed 6σ apart, C_1 and C_2 will have only a very small error resulting from competition between adjoining stations for the available population. The 50-foot interval between stations used by the North American Census of Small Mammals probably leads to a 10 to 20 percent underestimate of C_1 and C_2, and thus to an underestimate of density when C_1 is taken as the average number of animals per station.

The Trap-Day Index

A great many papers have been published which present information concerning the density of small mammals. It is rare to find an indication in these papers that the authors are aware that the procedures used may modify the results. Historically, knowledge of the density of small mammals was a byproduct of trapping to obtain specimens for museums. The collector customarily followed an irregular path through the habitat. Traplines were formed by placing traps at irregular intervals at points where it was thought specimens were most likely to be caught. These traplines were left set until the diminishing catch dictated removal of the traps to a new site. Relative density was expressed as

$$\frac{\text{number of animals caught}}{\text{number of traps}} \times \frac{\text{number of days}}{\text{traps were set}}$$

or, in other words, the number of animals per trap-day.

From data already presented, it is apparent that density of traps and the number of days traps are left set will markedly modify this index of density. Yet this index of density continues to be used by some investigators, for example, Beer and his co-workers (*23*), both for traplines and for grid trapping.

Relative Densities

Relative rather than absolute density has been assumed to suffice for solving many biological problems, but the area factor in density has been ignored. If all procedures are maintained constant, including the time over which samples are taken, it is assumed that the relative densities obtained will suffice for comparing different habitats or the same habitat at different times. However, these relative densities can be misleading. For example, on the traplines run by the North American Census of Small Mammals from 1948 to 1951, 1,901 male and 1,521 female deer mice (*Peromyscus*) were trapped. One might conclude from this that males in these areas were 25 percent more abundant than females, but this is probably not so. It is more likely that more males than females were caught because males have a larger home range than do females (*11*) and, therefore, more males than females are exposed to the traplines. Similar inaccuracies of assuming that relative densities are proportionate to true densities also apply to comparisons of the density of different genera or of the same genus in different habitats. Until much more is known concerning the influence exerted upon home range statistics by species, sex, and habitat, it is well to use caution in drawing conclusions from relative densities other than for those densities which concern a single species and sex from different times in the same habitat.

Summary

The principal objective of this monograph has been the development of a method of estimating density of small mammals in habitats sufficiently extensive so that a considerable part of a habitat lies peripheral to the habitat in which the sampling stations are located. Our major premise was that the expectation of capturing an animal at a particular station depends upon the distance of its center of activity from the trapping station. This premise required that an equation be found which approximated the density function of the animal about its center of activity. In general, the statistics of the home range were found to be stationary and to be approximated by the bivariate normal distribution of the density function:

$$f(x,y)\,dxdy=\frac{1}{2\pi\sigma^2}\,e^{-(x^2+y^2)/2\sigma^2}\,dxdy$$

where r is the radial distance of the point of capture at the coordinate, xy, from the center of activity.

The probability of finding an animal between the radii r and $r+dr$ about the true center of its home range is

$$f(r)dr=\frac{1}{\sigma^2}\,e^{-r^2/2\sigma^2}\,rdr$$

According to this equation, 0.394 of the captures fall within a distance of 1σ from the center of the home range, 0.8645 within 2σ, and 0.9888 within 3σ. Tables and figures are presented which enable us to calculate the proportion of expected captures within any band about the center of the home range.

Several methods are presented for estimating the standard deviation of this bivariate normal distribution from recapture data. An unbiased estimate of the standard deviation, σ, of the home range for a single animal in its simplest form is

$$\left[\frac{\sum_{j=1}^{K} r_j^2}{2(K-1)}\right]^{1/2}$$

where there are a K number of j captures.

For male *Reithrodontomys* the best estimate of the grouped $\sigma=52.7$ feet. Sigma varied significantly among animals, that is, all male *Reithrodontomys* do not have the same-sized home range. Therefore all r's had to be divided by their own σ's before radii from different mice could be pooled for comparing the observed and theoretical frequencies. These closely approximated each other.

It was further found that the number, c, of animals per unit area could be estimated by

$$\frac{C_1}{4\pi\sigma^2(1-C_2/C_1)}$$

where C_1 and C_2 are the average captures per trapping station for day 1 and day 2, respectively. Precautions to be considered when utilizing this equation include:

- The less one interferes with the normal pattern of movement in obtaining the observations upon which the home range parameter, σ, is based, the more accurate is this measurement.
- Inaccuracies in estimating σ will be minimized if the observations upon which σ is based are made over a span of time which is short in relation to the life span. This will increase the likelihood of excluding from the estimate animals which have shifted their center of home range.
- Sigma varies with sex, species, and habitat. Therefore, density measurements must include only one category of each of these conditions.
- Each sampling station must be adequate to provide the opportunity of sampling each animal which approaches it during each period of sampling.
- Sampling stations should be almost 6σ apart if underestimation of density arising from competition between sampling stations is to be minimized.
- Where C_1 and C_2 represent animals which have been removed from the habitat, the time between samplings should not exceed 24 hours, because C_2 in particular is likely to be augmented by animals which shift the centers of their home ranges toward the area about the sampling station that is becoming depleted of residents.
- Several samples of C_1 and C_2 must be taken in order to average out random error and variations due to changes in the weather.

The above approach to estimating density is most applicable to techniques of sampling involving removal trapping at fixed stations in extensive environments.

Where marking and releasing procedures are employed, the number, c, of animals per unit area may be estimated by

$$\frac{\text{antilog } a}{2\pi\sigma^2\,(1-\text{antilog } b)}$$

where σ is the standard deviation of the home range, log a is the intercept, and log b is the slope of a line formed by plotting the logarithms of the differences in captures between successive days, n, against $n-1$. For this method of estimating density to be valid two conditions must be met:

- Every animal approaching an observation or trapping station must have the opportunity of being sampled.
- Stations must be at least 6σ apart.

Details are presented of the development of the equations for estimating σ, the standard deviation of the home range, and for estimating density.

- Considerable discussion is devoted to how our formulation of home range may be employed for elaborating a more detailed understanding of this phenomenon and to how the habits of animals and the procedures of sampling affect the applicability of our equations for estimating density.

Several authors have estimated density by equations equivalent to

$$N=\frac{C_1}{1-C_2/C_1}$$

where N=initial population, and C_1 and C_2 are the numbers of animals taken on the first and second days of sampling. Such equations are applicable only in those special situations in which the probability of capture remains constant on both the first and second days as well as on following days. In general, these equations are not applicable when animals are removed from fixed stations about which some animals live closer than others.

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