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OF HETEROMYID RODENTS

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HOME RANGE DYNAMICS IN A POPULATION OF HETEROMYID RODENTS

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ABSTRACT.--Seasonal, sexual, and temporal aspects of home range for pocket mice (*Perognathus formosus* and *P. longimembris*) and kangaroo rats (*Dipodomys merriami* and *D. microps*) were analyzed from records accumulated over seven years of monthly censuses of the rodents in three 9-hectare enclosures and one similar area not enclosed in the Mojave Desert. The density function was used as a standard expression (in terms of sigma) to compare home ranges of different individuals, groups or species, or over time. Detailed analysis of 340 *P. formosus* in one enclosure showed that 16 shifted the home range location during the course of this study, and 99 were detected to make one or more long-distance excursions beyond their home range. Compilation of all data gives an average representation of home range for this species in this environment to be a circle of radius 31 meters, which will encompass 86 per cent of the animals' activity. This radius is the 2 sigma value computed from the data. Home range size differs between sexes and among years, with significant year by sex interaction. There is an inverse relationship between population density and home range size. Home range size is not related to body size in these four species which presumably occupy the same trophic level of the system. Home range shifts and excursions outside the established home range occurred most frequently in males and most frequently in the reproductive season.

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INTRODUCTION

The local distribution of animals is generally discussed in terms of home range (Burt, 1943) or territory (Noble, 1939). Often these are treated as static entities, with lines drawn around points of capture on a map, rather than as dynamic concepts. Populations of animals are continuously changing as new animals appear and as old ones leave or die, and these changes affect the size, shape, and distribution of home ranges (Stickel, 1946; Blair, 1940). Home ranges may undergo seasonal shifts or may be modified according to the availability of resources (Connell, 1954; Layne, 1954).

Several methods have been devised for estimating the boundaries, and thereby defining the area, of an animal's activity; these have been reviewed and discussed by Sanderson (1966). Ambrose (1969) indicated that the minimum area method might be the most accurate (of methods based on live trapping) if a sufficiently small trap interval is used.

A major improvement in the methods for describing home range was made by the application of statistical methods to data on the points of recapture. The density function (Calhoun and Casby, 1958) and the standard diameter (Harrison, 1958) are such methods. They have been criticized because they appear to treat the home range as circular, when in fact it may not be. The important point is that the center of activity (Hayne, 1949) is a mean of the points where activity has been detected, and it is therefore possible to compute a standard deviation of the mean, assuming the recapture points represent samples from a bivariate normal distribution. A theoretical circle with a radius of one standard deviation, or an area of one standard diameter, contains a given percentage of the animal's activity, whether or

not all of this area is used. The most important feature of such a method is that it provides a statistical measure of activity and makes possible comparisons among individuals, species, or populations (White, 1964).

METHODS

During a long-term radioecology study conducted in the Mojave Desert at the U.S. Atomic Energy Commission's Nevada Test Site, the small mammal populations in three enclosed study areas were individually marked and censused at monthly intervals. Over a seven-year period the accumulated records represent a total of 66,629 captures of 5,368 animals. Censuses were conducted by live trapping for three successive nights utilizing a 15-meter grid of 400 live traps. Although the study was not specifically designed for analysis of home range, the large number of records provides an opportunity to investigate some of the dynamics of space utilization by heteromyid rodents in this desert region.

The study areas are circular, encompassing nine hectares (22 acres), and surrounded by a rodent-proof fence. Special precautions regarding timing of the activation of traps and protection from direct sunlight were used to prevent trap mortality of the animals. At times of peak population densities, an additional 200 traps were added to the grid, an extra trap at alternate trap stations. (This occurred only in Plot B during August through October 1965 and June 1966.) Animals were marked by toe amputation or by metal ear tags. At each capture, information on identity, location, and physiological condition of animals was recorded. Immediately following each trapping period, the data were punched on Hollerith cards and subjected to a screening program which gave the opportunity to examine for errors in the information

recorded. A separate program was used to add new data to the accumulated file of information, thus keeping at all times a complete version of all recorded information available. For preliminary evaluation of the data, a program was written to select those animals which had been captured at a minimum of three different locations in the grid on a minimum of 10 different occasions and sort the records for those individuals meeting these criteria according to date and location of capture. We felt this was necessary for adequate description of a home range. The center of activity (Hayne, 1949) was also computed to indicate the animal's mean location within the grid. The resulting tables not only organized the data for convenient inspection, but also indicated any temporal shift of the locations where activity was detected, for example, a shift in the home range, or long-distance movements. Capture locations for individual animals were also plotted on a map of the grid with an IBM-XY plotter.

As an indication of the size of the home range of individual animals, the standard deviation of the normal distribution function (Calhoun and Casby, 1958) was computed for individual animals and for the species. This is based upon the distances between the computed center of activity and individual locations of capture, and gives the value of a radius within which the probability of the animal being present is 39 per cent. The value for an area of two standard deviations is 86 per cent and for three standard deviations is 99 per cent. This provides a means for comparing the areas utilized by different species, by different individuals at one season of the year, or by the same individuals in different seasons of the year or at different population densities.

The data were also tested to determine if they fulfilled the assumptions inherent in the method. Examination of the XY plots of 417 individual home ranges of *Perognathus formosus* reveals that for the most part they are more or less circular, not elliptical as in other species (Jennrich and Turner, 1969; Mazurkiewicz, 1969). Because the use of the "density function" as a description of animal activity assumes a circular bivariate normal distribution, it seemed advisable to test the distribution of recapture points for circularity. We analyzed the distribution of points around each center of activity for significant deviation from a uniform distribution, utilizing both Kuiper's modification of Kolmogorov's test and the modification of Smirnov's test as described by Batschelet (1965). Although it may at first appear inappropriate to test for a uniform circular distribution because this considers only the angles of recapture points from the center of activity and ignores the distance, it must be remembered that the center of activity is a computed center of gravity of all the recapture points and is therefore already weighted for distance of the various points from the center. In order to apply Kolmogorov's test we computed the cumulative distribution function of the recapture points for an animal and compared it to a uniform distribution, using the table of critical values given by Batschelet. Kolmogorov's test compares the maximum deviation between the two distribution functions, and Smirnov's test utilizes the mean square deviation. The density function assumes that when the recapture points are plotted, the location of a point on the X axis is independent of its location on the Y axis, or $\rho_{xy} = 0$. Another assumption is that the points are normally distributed along either axis and that the variance of one distribution is equal to the variance of the other, or $\sigma_x^2 = \sigma_y^2$. These

assumptions are checked by applying tests II and III as given in Calhoun and Casby (1958) to these data.

Long-distance excursions occur infrequently and represent exploratory sallies rather than part of the routine activity. For comparison of long-distance excursions with average movements, all distances of recapture points from the center of activity were converted to standard form Z (Calhoun and Casby, 1958). This relates the distance of recapture points from the center of activity to the standard deviation or sigma value for the individual. If the distance of a recapture location was found to be greater than five times the sigma value, that recapture was considered to be a long-distance excursion. When sigma was recalculated for comparison of home ranges, such a location was omitted from the computations.

RESULTS

Characteristics of combined recapture records.--The general distribution of recapture locations around the computed center of activity of the animals may be envisioned by reference to Fig. 1. In this figure a large number of records for many animals of the same species are superimposed on a single center of activity. The center of activity for the distribution of recaptures for each individual animal was placed at the center of the circle, and the recaptures were totaled accordingly. In this particular example, 10,795 captures of 417 animals were plotted, and the sum of captures for each separate location is indicated. The circle represents the total study area. The size of the squares superimposed on the circle is 15 meters. The value for sigma in this combined example is 19.83 meters. It can be seen that frequency of captures decreases rapidly with increasing distance from the

center. This value may be used to compute the total number or percentage of the total captures that occurred within given distances of the center of activity.

Home range shift.--Temporal shifts in home range by individual animals were best revealed by tabulating the series of recaptures for each individual animal in a form that showed both the location and the time of capture. XY plots of the distribution of recapture points were of limited value because they failed to show the time sequence of recapture points. Two examples of such tables are shown in Tables 1 and 2. Table 1 shows the recaptures of male *Perognathus formosus* No. 1102 from the summer of 1962 through 1966. The pattern of distribution indicates a gradual expansion of the home range of this individual. New locations were added progressively, but the old locations were never abandoned with possibly one or two exceptions. Table 2 is an example showing the captures of male *P. formosus* No. 1220, indicating two shifts in the home range of this animal. Four captures in 1962 revealed that as a juvenile it visited three locations in the grid. In 1963 a new set of seven locations was used, and those locations used in the previous year were abandoned. This continued through 1964, following which there was another shift in the animal's activity. Those locations utilized in 1965, 1966, and 1967 compose a distinct set of 16 locations not utilized before by the animal, to the exclusion of the previous locations.

Our evaluation of home range of the pocket mouse, *Perognathus formosus*, is based principally upon 10,167 captures of 340 different individual animals in one of the study plots (Plot A). These are the individuals whose records met the criteria of being captured in three or more different locations on 10 or more different occasions. Those records for animals

which did not meet the criteria were not included in these analyses. A total of 16 individuals shifted their home ranges during the course of this study. Some animals showed one or more long excursions from their home range without demonstrating a permanent shift in their location of activity. A total of 99 individuals made one or more such long-distance excursions; of these 10 made two such excursions and one made three excursions.

A sample of the combined XY plots of four individual animals is shown in Fig. 2. The large circle in the figure represents the boundary of the study area or the fence around the field plot. The X and Y axes represent trap locations, with an interval of 15 meters. Capture locations of different individuals are shown by different symbols. Each symbol represents one location of capture. The number in the symbol indicates the number of times the animal was captured at that particular location. The computed center of activity (CCA) is indicated for each animal by an X. Animal No. 1101, represented by triangles in Fig. 2, shows a shift in the home range. If all locations of capture are used to compute a single center of activity, the location of this is shown with an asterisk. Examination of the temporal sequence of captures, however, reveals that these locations should be divided into two separate home ranges; each center of activity for these is shown by the appropriate X. This individual also shows an example of a long-distance excursion movement. This appears as a triangle in the lower right portion of the grid figure.

The utilization of different portions of the home range may change with time, even though the animal does not demonstrate a shift in the home range area. Fig. 3 shows the changing utilization of space within the home range of one animal over a five-year period, 1962 to 1966. The curved line

represents the fenced boundary of the enclosure. The records from 1962 are composed of five captures at a single location shown by a plus (+) symbol. The circles represent the locations of capture during 1963, and the numbers by the circles indicate the number of captures for each location. In 1964 the locations of capture are indicated by triangular symbols. Locations of capture in previous years are shown by solid dots. Similarly, the locations of capture in other years are shown by different symbols; in each case the locations of capture in previous years are shown by solid dots. In each year some new locations were added, and some of the old locations were not revisited. The trend in this case, however, fails to reveal a general shift in the area of the animal's activities.

Sigma as a representation of home range.--Using the computed value of sigma (Calhoun and Casby, 1958) as an index of the home range size, it is possible to make comparisons among sexes, plots, and seasons and to examine the effects of shifts in ranges and long-distance excursions by individuals. The home range size of *Perognathus formosus* in terms of sigma is indicated by the results summarized in Table 3. When those home ranges which represent a shift in an animal's activity over time are divided into the two separate home ranges that they represent, the computed size of the home range is reduced. A further reduction results when those infrequent long-distance excursions which are occasionally made by these animals are deleted from the computation. It has been demonstrated (Wierzbowska and Chelkowska, 1970) that this method is sensitive to such movements. On the basis of these results the approximate average home range size would be represented by a circle with a radius of 15.5 meters. A circle of this size, representing one sigma, would include the area in which an animal spends approximately

39 per cent of its time. A circle of radius 31 meters would therefore include the area in which an animal spends 86 per cent of its time, and a circle of radius 46.5 meters an area in which the animal spends essentially 100 per cent of its time.

The assumption that the points of capture are approximately equally distributed around the center of activity may be tested to see if they differ significantly from a bivariate normal distribution. Two tests given by Calhoun and Casby (1958) were utilized on the capture locations for each individual animal considered in the above analyses. The point of capture in each case is evaluated according to the distance from the center of activity on the two coordinates, X and Y. It is assumed that the variance in the X direction is equal to the variance in the Y direction. It is also assumed that there is no correlation between the X and Y coordinates for individual points. Results of the tests are summarized in Table 4. Of primary interest is the number of animals whose individual captures passed both tests or were rejected by both tests. When all cases are considered in the analyses, 146 animals or 43 per cent passed both tests. A total of 58, or 18 per cent, was rejected by both tests. This rate of failure to meet both criteria for the bivariate normal distribution seems fairly high. However, when the captures for individual animals were examined according to their time sequence, it became apparent that some of the results represented shifting ranges, as certain portions of the home range were no longer used and new portions were added. Therefore, some of these could be appropriately divided into two separate home ranges. In addition, long-distance movements to points well outside the normal range of activity, which occurred infrequently, were deleted from computations. With these modifications of the

data, the tests were again applied. Results are also shown in Table 4. In this case, 181 individuals, or 53 per cent, passed both tests, and 27 individuals, or 8 per cent, were rejected by both tests, a considerable improvement in the fit to a bivariate normal distribution.

Results of tests for circular distribution of the capture points around the centers of activity of individual animals are shown in Table 5. Again there were two tests deemed appropriate for the analyses of these data. When all captures for animals meeting the minimum criteria of 10 total captures in three locations were included in the analysis, the data for 265 animals, or 78 per cent, passed both tests; and those for eight animals, or 3 per cent, were rejected by both tests. These results indicate a sufficient similarity to a circular distribution so that the methods we have applied seem appropriate. When long-distance movements were removed from consideration and shifted home ranges were divided, there was no significant change in the results from application of these tests.

We have chosen the value of 2 sigma as the best representation of the distribution of animal activity around the computed center of activity. As has been stated, 2 sigma is the 86 per cent probability level, or should theoretically include 86 per cent of the animal's recaptures. Some examples to illustrate this are shown in Fig. 4. Here the circles representing the 2 sigma values for three individual animals are plotted on separate maps of the grid, along with the shaded area representing the minimum area of animal activity as indicated by recaptures. It can be seen that most of the shaded portion is encompassed within the circle, with some additional area also included. If such a circle can be used to represent the activity of animals over time, then the relationship of a number of animals can be illustrated

by a diagram containing the center of activity and corresponding 2 sigma value circles of those animals that were living simultaneously within one grid. An example of this is shown in the lower right portion of Fig. 4, where circles representing three contemporaneous animals are presented. The effective utilization of various portions of the habitat may be illustrated by such means, as well as the degree of overlap of habitat utilization.

The relationship of all animals present in one grid at one time is diagramed in Fig. 5 and 6. One of these represents the total *Perognathus formosus* population present in Plot A in the summer of 1966; the other represents those animals present in the same plot during the winter months of 1966 and 1967. A separate value sigma for each individual was used in each case. The plot representing the summer months includes territories of 125 individuals, that for the winter months 50 individuals. The population densities of the grid were somewhat greater in each case, due to elimination of those individuals whose records were insufficient for these computations. In the summer the population densities ranged between 142 and 157 individuals; in the winter the density ranged from 82 to 135 individuals.

Significance of changing sigma.--The dynamic aspects of home range in this species are illustrated by the changes in sigma with season, with sex, with plot, with species, and with population density. Results of analysis of variance of individual sigma values indicates the difference between years and sexes is highly significant (Table 6). There is also a significant difference in the sigma values for different plots and an indication of year by sex interaction. Included in this analysis were the results from three plots (A, B, and C), two sexes, and three years (1966, 1967, and 1968). Winter data for this species were considered inadequate for this type of

analysis. This stems primarily from the fact that these animals are inactive during the cold season, resulting in a lack of records.

There is apparently an inverse relationship between the size of the home range and the population density. When population densities are high, the value of sigma is low, and vice versa. When the data are reduced to seasonal averages, however, analysis fails to indicate statistical significance in this relationship. Although the sigma values for males and females fluctuate together, the home range of females is invariably smaller than those of males.

Results of computation of group sigma values are presented in Table 7. Separate values are given for males and females in the different seasons where data were sufficient for such computations (at least five animals fulfilled criteria for inclusion), and values are given for both sexes combined. In addition, there are summaries across seasons by plots.

Comparison of group sigma values for the different species of heteromyids involved in this study are given in Table 8. Home ranges of other species, including the small *Perognathus longimemberis*, exceed those of *Perognathus formosus*. It is evident that home range size is not correlated with animal size. The smaller of two pocket mouse species has the larger home range requirement. The same is true with the kangaroo rat. *Dipodomys merriami* showed a higher value for sigma than did the larger *D. microps*.

Behavior and home range dynamics.--An analysis of the seasonal occurrence of long-distance excursions to points outside the normal home range made by individual animals provides some indications of the relationship of these activities to the life history of the animal. Frequency of excursions tabulated by the month in which they were detected is presented in Table 9. It

is apparent that the frequency is highest in the spring months of the year and declines as the season progresses. This is quite apparent in the three fenced study areas, but fails to appear in results from the unfenced study area (Plot D). This is probably due to the fact that animals in the unconfined population can readily make excursions beyond the boundary of the study area and thereby go undetected. These results suggest a correlation between reproductive activities and long-distance excursions.

When the frequency of long-distance excursions is evaluated with relationship to external manifestations of sexual activity of the animals (Table 10), it is evident that the sexually active male animals predominate among those making such movements. Nearly 50 per cent of all long-distance excursions detected over this period were made by sexually active adult males. These results also indicate that sexually active adult females are comparatively sedentary. The least amount of movement was made by this group of animals. Sexually inactive animals, both males and females, both juveniles and adults, made approximately the same relative number of excursions.

Shifts in the home range may be similarly correlated with sexual activity of the species (Table 11). This refers to abandonment of an old home range and establishment of a new one. As is the case with excursion movements, the home range shifts are evidently associated with the reproductive season, and such shifts are made principally by the males of the population.

DISCUSSION

The home range of these rodents can be adequately described by a circular bivariate normal distribution. Home ranges may appear elliptical when infrequent long-distance excursions are included in the analysis, or when

temporal shifts are not considered. The method used here permits evaluation of temporal changes in home range location and size. These temporal and spatial changes may occur by gradual expansion of the area utilized or by relocation of the area of activity. Home range size differs between sexes, among seasons, with population density, and among species.

These results suggest a physiological basis for home range and movements. The spatial relationships among individuals of a population are determined by relationships to other individuals in the population, rather than by resources available in the environment. (These questions and supporting data are explored further in a manuscript in preparation.) From this it may be concluded that the size of the home range is sufficiently large to encompass the resources and habitat requirements of the individual. The minimum size of home range observed over a period of time probably represents that minimum area which can sustain the individual. Enlargement of the home range during periods of population decline probably reflects changes in social interaction or frequency of interaction more than it reflects changes in the quality of the environment. Similarly, changes in activity with physiological conditions reflect more the changing intraspecies interactions than changing factors of the environment. In summary, then, it may be stated that home range dynamics within these species is primarily a manifestation of behavioral interaction among the individuals of the species.

The home range size of *Perognathus formosus*, and probably for other heteromyid rodents, evidently has some lower limits beyond which it cannot be further compressed. Such a lower limit, or minimum area, would indicate that home range in these animals might serve to regulate population size (Klopfer, 1969). This may be a direct correlation, or it may simply be

that there is a relationship between the forces that control population size--perhaps social interaction and behavior--and those which govern home range size.

We fail to find evidence to indicate that the home range is other than circular, as reported by Mazurkiewicz (1971) and by others. Even that well-documented study indicates that 30 per cent of the home ranges are circular.

There is evidence of a certain flexibility in home range size, particularly regarding males. The evidence strongly indicates, however, the generally high degree of stability of home ranges in *Perognathus formosus*. Only about 5 per cent of the *P. formosus* shifted home range over the years of this study. A high degree of stability for established home ranges has been reported for *Peromyscus leucopus* (Stickel and Warbach, 1960) and for the chipmunk (Yerger, 1953). In contrast, the microtine rodents show a high frequency of short-term shifts of home range, as in *Microtus pennsylvanicus* (Ambrose, 1969) and *Clethrionomys glareolus* (Mazurkiewicz, 1971). About 40 per cent of the *Clethrionomys* population shifted locations between trapping periods 1.5 months apart.

The average size of the home range in *P. formosus* is approximately 5500 m². For *Peromyscus leucopus* it seems to be about 1800 (♀) to 4000 (♂) m² in results presented by Stickel and Warbach (1960), 2200 (♀) to 2600 (♂) m² in *Apodemus sylvaticus* (Brown, 1956), but only 1000 (♀) to 1500 (♂) m² in the chipmunk (Yerger, 1953). In general, microtines have smaller home ranges: *Microtus pennsylvanicus* 200 up to perhaps 800 m² (Getz, 1961; Ambrose, 1969), *Microtus agrestis* 500 (♀) to 970 (♂) m² (Brown, 1956), and *Clethrionomys glareolus* approximately 1600 m² (Brown, 1956) or 3000 m².

(Mazurkiewicz, 1971). There is agreement among many workers that males have larger ranges than females.

There is no evidence of dominant males that shift ranges or have unusually large ranges, as suggested by Brown (1966). She states that such a dominance hierarchy results from constant intraspecific strife. The intolerance of one heteromyid rodent for another of the same species is well known, hence the extreme difficulty of establishing reproducing colonies under laboratory conditions (Hayden, Gambino, and Lindberg, 1966). It is probable that under natural conditions intraspecific contact results in such intense repulsion that there is insufficient individual contact to permit establishment of a dominance hierarchy.

Because heteromyid rodents have strong interference elements in their competitive relationship and also rather rigid dispersion mechanisms, they are among those rodents which have relatively low replacement rates and greater population stability (Miller, 1967). The other class of rodents would be those with high biotic potential and considerable tolerance for crowding and consequent extreme fluctuations in population density. We consider heteromyid rodents among those manifesting greater population stability in spite of the evidence of great fluctuations in density (French, Maza, and Kaaz, 1969). These fluctuations result rather from the great extremes of environmental conditions encountered by these desert rodents. They respond to unfavorable growing conditions, particularly primary production, by complete inhibition of reproduction in certain seasons (French, Maza, and Aschwanden, 1967). They are specifically adapted to tolerate these extremes, as evidenced by their ability to increase the duration and frequency of periods of torpor (Tucker, 1966). Field evidence from marked

animals indicates the ability of these small creatures to survive unusually long periods of unfavorable conditions (French, Maza, and Aschwanden, 1966).

It should therefore not be surprising to find that these rodents had evolved special behavioral mechanisms regarding home range which would better enable them to tolerate their extreme environment. It was evident that certain portions of the study areas were more highly favored than others in our study. The minimum area of home range was maintained, however, by a higher tolerance of overlap in adjacent home ranges during periods of high population density. The behavioral adjustments that foster this remain obscure. By direct observation, we have determined that different individuals of the same species and members of different heteromyid species may on occasion utilize the same burrow, at least for brief periods. In addition, we have observed that *Perognathus formosus* will climb into the branches of low shrubs while foraging, thus adding a dimension to its home range. These highly pugnacious animals may actually avoid contact with one another as a mechanism of tolerance.

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TABLE 1.--Recapture records in time and space of *P. formosus*, No. 1102, Plot A, adult male; Life Span: 8-62 to 11-66, 51 months. There were 24 different locations; computed center of activity was 81.725 and 75.938; individual sigma value was 19.4 m. Center of grid is at Location 6666. Season (winter, spring, summer, and fall) designated as W, S, S, F.

Location	1962				1963				1964				1965				1966				Captures
	W	S	S	F	W	S	S	F	W	S	S	F	W	S	S	F	W	S	S	F	
8276			1	4			1	2				1									9
8074					1		1														2
8076						1	1			1	1	1			1		1	1			8
8278						1	2	1						1			1	4	2		12
8078						1				1		1					1				4
7876							1										2				3
8070							1														1
8478							1							4		2		2	1		10
8472								1		1											2
8474								1		1											1
8272								1		1		1									2
8072								1		1											1
8274											2	1		2	2		1				8
8470											1										1
8270											1										1
8280												1							2		4
7874														1							1
8468															1						1
8871															1						1
8670															1						1
8476															1						1
7484														1		3					4
7880																	1				1
7272																	1				1
Total Number of Captures																					80

TABLE 2.--Captures of adult male *P. formosus*, No. 1220 Plot A; Life Span: 8-62 to 5-67, 58 months. There were 29 different locations; computed center of activity was 74.937×81.013 ; individual sigma value was 39.7 m.

Location	1962				1963				1964				1965				1966				1967				Captures
	W	S	S	F	W	S	S	F	W	S	S	F	W	S	S	F	W	S	S	F	W	S	S	F	
5280	1	1																							2
7680		1																							1
6872		1																							1
8080					3	1			1	1	3	1													10
8078					1				1			2													4
8278					3						1	1													5
8082					1	1					1														3
7882					1																				1
7880						1			1	1	3														6
7878						2				1															3
8076										1		1													2
8280											1	1													2
7286													1	2											3
7248													1												1
7084													1				1	1	2						5
6884													1												1
7284													1				1	3	3		2				10
7484													2												2
7486													1				1								2
7686													1												1
7482																	1								1
7684																	1								1
7282																	1		2		1				4
6882																	1								1
7476																	1								1
6888																	1								1
7082																		1			1				2
7086																					2				2
7280																					1				1
Total Number of Captures																									79

TABLE 3.--*Perognathus formosus* home range size (meters) in terms of sigma (Calhoun and Casby, 1958) for four study areas from 1962 to 1968.

Plot	Total Population	Number of Animals	Number of Captures	Sigma (meters)	Data Included
A	601	340	10,167	18.9	
B	787	567	17,678	18.2	All that met criteria of 10 captures and three different locations.
C	525	345	8,632	22.3	
D	976	195	3,371	17.5	
A	617	345	10,110	17.0	As above, with individuals that had shifted home ranges split and considered as distinct individuals in each range.
B	790	570	17,678	17.8	
C	531	350	8,629	20.6	
D	980	194	3,359	16.6	
A	617	337	10,005	14.9	As above, but with all single long-distance excursions deleted.
B	790	562	17,377	14.1	
C	531	342	8,496	18.6	
D	980	192	3,326	14.5	

TABLE 4.--Results of tests of equality of variance along the X and Y coordinates and of lack of correlation between X and Y coordinates for points of capture of *P. formosus* in relation to the centers of activity for individual animals.

Data Included		Test II $\sigma^2_x = \sigma^2_y$			
All captures	Test III Correlation Coefficient = 0		Pass	Reject	Total
		Pass	146	67	213
		Reject	69	58	127
		Total	215	125	340
Long-distance excursions deleted; shifted home ranges divided			Pass	Reject	Total
		Pass	181	63	244
		Reject	70	27	97
		Total	251	90	341

TABLE 5.--Results of tests of circular distribution of capture points of *P. formosus* around centers of activity.

	Smirnov Test		
	Pass	Reject	Total
Kolmogorov Test	Pass	265	303
	Reject	29	37
	Total	294	340

TABLE 6.--Analysis of variance of sigma values for plots (A, B, C), sexes, and years (summers of 1966, 1967, 1968).

Source	Sum Squares	DF	Mean Square	F
Plot	503.81	2	251.91	3.33*
Sex	1994.07	1	1994.07	26.37**
Year	2157.21	2	1078.61	14.26**
Plot × Sex	4.79	2	2.39	0.03
Plot × Year	705.91	4	176.48	2.33
Sex × Year	517.11	2	258.56	3.42
Plot × Sex × Year	42.94	4	10.74	0.14
Error	81517.66	1078	75.62	

* Significant at $P = .05$.

** Significant at $P = .01$.

TABLE 7.--*Sigma (meters) computed for P. formosus in different seasons (S = Summer, W = Winter) and study areas (A, B, C, D).*

Year	Season	All Individuals				Males				Females			
		A	B	C	D	A	B	C	D	A	B	C	D
1963	S	12.6	--	--	--	12.7	--	--	--	13.5	--	--	--
1964	S	17.5	16.4	22.9	--	17.8	15.8	21.5	--	18.1	16.1	25.6	--
1965	S	--	21.8	22.2	--	--	23.1	31.7	--	--	20.0	13.2	--
1966	W	19.1	14.4	24.3	--	22.3	14.9	28.2	--	12.5	10.1	15.6	--
1966	S	14.5	12.4	11.8	12.3	15.9	12.6	14.2	11.6	13.2	10.5	9.2	14.2
1967	W	13.4	9.0	--	--	15.0	--	--	--	10.2	--	--	--
1967	S	13.1	9.4	10.6	15.3	13.7	6.8	11.2	18.7	13.0	10.6	11.7	13.0
1968	S	14.0	15.2	19.5	14.4	15.8	16.0	22.7	16.1	13.0	12.6	18.1	13.0
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Summary: All Seasons		14.9	14.1	18.6	14.5	16.2	14.9	21.6	15.5	13.0	13.3	15.6	13.4

TABLE 8.--Sigma (meters) computed for four major species according to season (S = Summer, W = Winter) with data from all plots combined (Pefo = *Perognathus formosus*, Pelo = *P. longimembris*, Dime = *Dipodomys merriami*, Dimi = *D. microps*).

Year	Season	All Individuals				Males				Females			
		Pefo	Pelo	Dime	Dimi	Pefo	Pelo	Dime	Dimi	Pefo	Pelo	Dime	Dimi
1963	S	10.0	--	27.9	25.5	10.2	--	--	20.2	11.0	--	--	29.5
1964	W	31.0	--	--	22.7	30.6	--	--	21.3	32.7	--	--	24.6
1964	S	16.2	30.5	41.4	29.7	16.9	31.6	46.4	30.2	16.8	--	44.3	29.0
1965	W	--	--	48.9	22.3	--	--	--	19.9	--	--	--	25.1
1965	S	20.9	--	39.4	39.1	27.1	--	--	39.7	16.8	--	--	38.3
1966	W	14.8	--	47.3	32.5	18.0	--	--	41.1	8.9	--	--	23.8
1966	S	10.3	21.4	28.4	15.8	12.3	14.6	31.6	14.9	9.1	40.5	33.0	16.2
1967	W	10.0	--	31.6	19.7	11.6	--	31.7	19.9	7.7	--	--	19.2
1967	S	12.2	11.5	38.8	27.8	9.6	12.9	40.9	27.7	9.4	13.7	--	27.8
1968	W	--	--	--	30.7	--	--	--	37.5	--	--	--	--
1968	S	13.2	12.5	32.1	25.4	15.5	12.4	36.2	27.1	11.8	16.0	34.1	23.3
<hr/>													
Summary: All Plots and Seasons		15.4	19.0	37.3	26.5	16.9	17.9	37.4	27.2	13.8	20.1	37.1	25.7

TABLE 9.--Long distance excursions by *P. formosus* in the four study areas, 1962 to 1968 (48 of the 354 individual animals moved more than once).

Month	Study Area				Total	Season
	A	B	C	D		
12	0	1	3	0	4	Winter
1	1	0	2	0	3	
2	4	8	2	1	15	
3	23	52	21	2	102	Spring
4	17	27	12	0	52	
5	9	17	11	6	42	
6	17	15	4	4	44	Summer
7	8	20	8	2	35	
8	12	7	3	0	21	
9	4	5	7	1	17	Fall
10	2	7	1	0	11	
11	2	5	1	0	8	
	99	164	75	16	354	Total number of excursions
	340	567	345	195	1447	Total number of animals in sample

TABLE 10.--Long-distance excursions of *P. formosus* in the four study areas August 1962 to December 1968, by sex, age, and sexual activity. (Total number of animals in each category in parentheses.)

	Male			Plot	Female			Total
	Inactive		Active		Inactive		Active	
	Juvenile	Adult	Adult		Juvenile	Adult	Adult	
	14 (133)	15 (179)	49 (107)	A	6 (112)	13 (161)	2 (73)	99 (340)
	15 (204)	20 (263)	86 (194)	B	16 (266)	20 (304)	7 (157)	164 (567)
	15 (142)	6 (167)	30 (111)	C	6 (163)	14 (183)	4 (92)	75 (345)
	3 (76)	1 (106)	5 (62)	D	4 (60)	3 (86)	0 (49)	16 (195)
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Total	47 (555)	42 (715)	170 (474)		32 (601)	49 (734)	13 (371)	354 (1447)

TABLE 11.--Shifts in location of home range of 29 *P. formosus* between 1962 and 1968.

Plot and Animal Number	First Home Range		Season in Transit (as in Table 9)	Second Home Range		Sex
	Months Resident	Last Capture		First Capture	Months Resident	
Plot A						
4	28	11-64	Wint.-Sprg.	05-65	16	♂
204	3	10-62	Fall-Sprg.	04-63	6	♂
210	26	10-64	Fall-Wint.	03-65	6	♂
220	3	10-62	Fall-Sprg.	04-63	13	♂
225	34	05-65	Spring	06-65	28	♂
404	5	12-62	Wint.-Sprg.	05-63	4	♂
432	3	10-62	Fall-Sprg.	05-63	7	♂
1101	33	05-65	Spring	06-65	30	♂
1220	27	10-64	Fall-Sprg.	05-65	25	♂
1305	5	12-65	Winter	02-65	2	♂
1423	5	02-62	Winter	03-66	12	♂
2145	20	01-68	Winter	03-68	5	♂
2215	5	11-66	Winter	01-67	4	♂
3002	6	10-67	Fall-Wint.	03-68	3	♂
111	3	10-62	Fall-Sprg.	03-63	14	♂
3042	16	11-67	Fall-Sprg.	03-68	4	♀
Plot B						
1040	29	10-67	Fall-Wint.	01-68	9	♂
4441	18	10-67	Fall-Sprg.	03-68	8	♀
1041	14	11-64	Fall-Sprg.	06-65	13	♀
Plot C						
41	20	10-65	Fall-Wint.	02-66	2	♂
120	7	10-64	Fall-Wint.	12-64	7	♂
132	13	05-65	Sprg.-Sum.	06-65	24	♂
1040	13	02-66	Wint.-Sprg.	03-66	18	♂
1153	17	09-67	Fall-Sprg.	03-68	8	♂
1001	7	02-66	Wint.-Sprg.	03-66	20	♀
Plot D						
51	5	07-64	Sum.-Sprg.	04-65	2	♂
205	8	02-66	Wint.-Sprg.	03-67	2	♂
3220	6	12-66	Wint.-Sprg.	93-67	11	♂
54	6	09-64	Fall-Sprg.	03-65	2	♀

FIGURE TITLES

Fig. 1.--Cumulative records of capture of 417 *P. formosus* plotted on a single center of activity ($\sigma = 19.83$ m).

Fig. 2.--Plot of all captures of four individual *P. formosus* superimposed on a map of the circular fenced study area.

Fig. 3.--Changing utilization of space by one *P. formosus* over a five-year period.

Fig. 4.--Relationship of circular 2σ areas to actual recapture points in *P. formosus* and the relationship of such circular areas for different individuals to each other.

Fig. 5.--Relationship of home ranges of 125 *P. formosus* present in Plot A during the summer of 1966.

Fig. 6.--Relationship of home ranges of 50 *P. formosus* present in Plot A during the winter of 1966-67.

Fig. 1

Fig. 2

P. formosus

male

Plot 2

Fig. 3

Fig 4

Fig. 5

Fig. 4