

HOME RANGE DYNAMICS OF RODENTS IN A SAGEBRUSH COMMUNITY

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ABSTRACT.—Home range sizes were estimated seasonally for *Microdipodops megacephalus* and *Perognathus longimembris* and biweekly for *Dipodomys merriami*, *D. ordii*, *D. panamintinus*, *D. microps*, and *Peromyscus maniculatus*. Mean estimates are also presented for *Reithrodontomys megalotis* and *Onychomys torridus*. Principal component analysis was used to calculate home range values because of its ability to deal with a wide variety of home range configurations. All species showed great variability in home range size throughout the year. Shape of home range was similarly variable, although most species tended towards elliptical movement configurations. The heteromyids showed consistency in annual composite home range areas (0.33–0.49 ha) regardless of body size. The generally smaller cricetine rodents exhibited much larger composite home range areas (0.95–1.42 ha). Emphasis is placed on the utility of point-in-time estimates of movements rather than obtaining a single home range value, which subordinates the dynamic nature of small mammal movements.

Recent reviews of the concept of home range in mammals have described the definitions, techniques, analyses, and factors affecting size of those movements (Brown, 1966; Jewell, 1966; Sanderson, 1966). There is little agreement in dealing with the concept of home range and a total lack of continuity from one study to another in data collection methods. This lack of standardization negates the formation of meaningful generalizations concerning such aspects as causes of variations in size and shape intra- and interspecifically, particularly where small mammals are concerned. The formation of pragmatic, statistical models of mammal movements are paramount to clearly understanding functional processes in activity, foraging, population regulation, social structure, and energy flow in these communities.

The present report is a portion of a larger study dealing with a rodent community in the sagebrush desert of west-central Nevada (O'Farrell, 1973). This particular community is striking in that 12 species of surface-active, nocturnal rodents occurred on a 2.7 hectare plot. The purpose of the present paper is to describe the intraspecific variability in home range size and the dynamic nature of home ranges throughout the year. A standardized method is presented for data collection and analysis. The emphasis is to maximize data obtained while minimizing disturbance to the animals. The object is not to secure a few precise area estimates, but to obtain a general index of magnitude of movements for the population at given points in time. These data can then be used to evaluate the role of movement and spacing patterns in determining behavioral interactions within small mammal communities.

MATERIALS AND METHODS

The study area is located at the northern end of Warm Springs Valley, about 40 km N Sparks, Highway 33, Washoe County, Nevada, as described by O'Farrell (1974). A detailed description

of the vegetation and physical features of the area will be presented in a later paper dealing with dispersion and social interactions of sagebrush rodents.

Although there were 12 species of nocturnal, surface-active rodents present during the study (O'Farrell, 1974), sufficient recapture data were not obtained for all species. Therefore, home ranges will be presented for the following rodent species: *Perognathus longimembris*; *Microdipodops megacephalus*; *Dipodomys merriami*; *D. ordii*; *D. panamintinus*; *D. microps*; *Reithrontomys megalotis*; *Onychomys torridus*; *Peromyscus maniculatus*. Due to seasonal occurrence of some species, changes in trappability affecting recaptures, and extirpation, the data are summarized in varying time intervals.

In order to maximize the number of recaptures for point-in-time (3 day) estimates of home range, the following regimen was utilized: a Sherman live trap was placed at each station of a 12 by 12 station grid encompassing 2.7 ha. Interstation spacing of 15 m was utilized. Trapping was conducted from 18 January 1972 to 7 January 1973 for six nights each month (on three consecutive nights during the first part and again in the latter part of the month). Traps were opened and baited with rolled oats at sunset and checked at 2-h intervals throughout the night. For each animal captured, trap number, time, species, sex, relative age, reproductive condition, and weight were recorded. All animals were toe-clipped for identification.

Home range was calculated two separate ways using a program designed by Robert H. Gardner (Savannah River Ecology Laboratory; personal communication). Circular home range was determined using the calculations of Calhoun and Casby (1958) for a circle encompassing an area where the probability of the animal being present is 0.95. The radius of this circle is a 2.45-sigma radius as described by O'Farrell et al. (1975). Home range was also calculated using the principal component method (Jennrich and Turner, 1969; Mazurkiewicz, 1971), which yields a 95% probability area. The latter method is preferable because it can deal with a wide variety of home range configurations and is particularly suited for measuring elliptical home ranges, similar to those described by Jennrich and Turner (1969) and Mazurkiewicz (1971). The circular method is only satisfactory when the recapture distribution varies little from a circular pattern, and it is never more accurate than the principal component method.

In addition, the center of activity (Hayne, 1949) was calculated and used in conjunction with sigma values (Calhoun and Casby, 1958) to detect significant temporal shifts in home range (Maza et al., 1973). The ratio of major and minor axes from the principal component method were obtained and examined as an index of circularity of home range configuration. When the ratio of axes equals one, the home range is circular, but the ratio increases as the shape becomes more elliptical (Mazurkiewicz, 1971).

Whenever the number of recaptures was sufficient, home ranges were calculated on a bi-weekly basis. Recaptures of *D. microps* were sparse enough to warrant combining trapping periods to yield monthly home range values. Likewise, *P. longimembris* and *M. megacephalus* were grouped into seasonal sets: spring (March, April, May); summer (June, July, August); fall (September, October, November). Recaptures greater than five were considered sufficient for a home range calculation, although estimates may be obtained with less than five recaptures. Home ranges based on less than five recaptures were incorporated if they fell within the range of values based on greater than five recaptures. Because the purpose of this study was to examine the dynamic trends in space utilization rather than to obtain a few static estimates of area occupied throughout the year, this was deemed reasonable. The proportions of home range estimates based on the frequency of recaptures are given in Table 1.

Non-parametric statistics were used to test for significant temporal trends (runs test for randomness) and significant sexual differences (Wilcoxon sign rank test) because of the extreme variability and low sample size encountered each trapping period.

RESULTS

Home Range Estimations

The seasonally active pocket mice, *Microdipodops megacephalus* and *Perognathus longimembris*, did not yield sufficient recaptures to allow home range estimations on a biweekly basis. Monthly summation was also impractical; therefore, home range estimates were obtained on an individual basis by combining seasonal recaptures (Fig. 1). Sample sizes in some cases are small but are considered to yield realistic

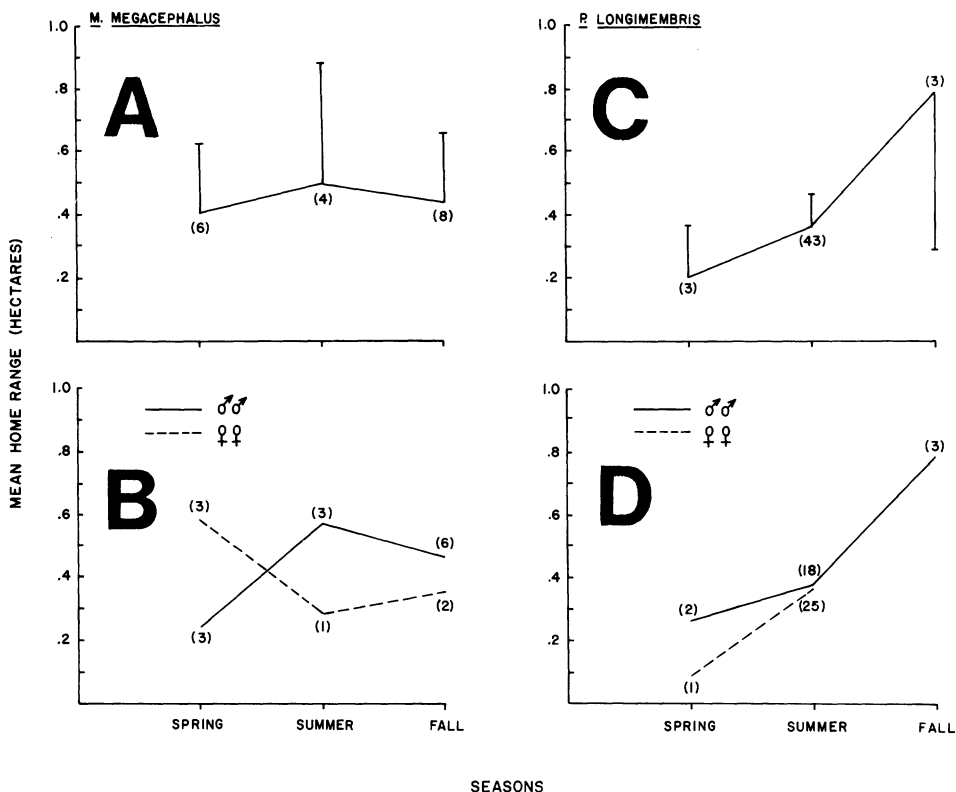


FIG. 1.—Mean home range estimates (95% probability ellipses) for *Microdipodops megacephalus* and *Perognathus longimembris*. The upper figures are sexes combined. Number of individuals used to calculate each mean are shown in parentheses. The bars on the upper figures represent 2 SE from the mean.

trends. For example, in summer there is only one value for female *M. megacephalus* because only one female was captured. Mean home range for *M. megacephalus* remained relatively constant (Fig. 1A), although males and females exhibited opposing trends (Fig. 1B). The variation within each seasonal grouping was considerable.

The trends for *P. longimembris* varied from those of *M. megacephalus* by constant increase through the year (Fig. 1C); variability among fall individuals was extreme. This corresponded to the time when final preparation for hibernation took place with *P. longimembris* entering hibernation much earlier than *M. megacephalus* (O'Farrell, 1974). Except in the fall, *P. longimembris* tended towards a slightly lower mean home range than did *M. megacephalus*. Variations due to reproductive activity were not observed in either species; only a few males showed signs of becoming reproductively active and females were not observed in estrus, pregnancy, or lactation.

In order to examine the full extent of the dynamics of rodent movements, mean home range values were calculated and plotted at biweekly intervals (Figs. 2, 3, and 4); *D. microps* is plotted on a monthly basis. For *Dipodomys merriami* (Fig. 2A), there appears to be a trend toward an increase in home range size in the late spring with a subsequent major increase in the fall. It is important to note the extreme variability between individuals for any given date, particularly with regard to certain individuals. In most cases, there are several individuals throughout the year that show exaggerated movements compared to the rest of the population. However, it is not always the same

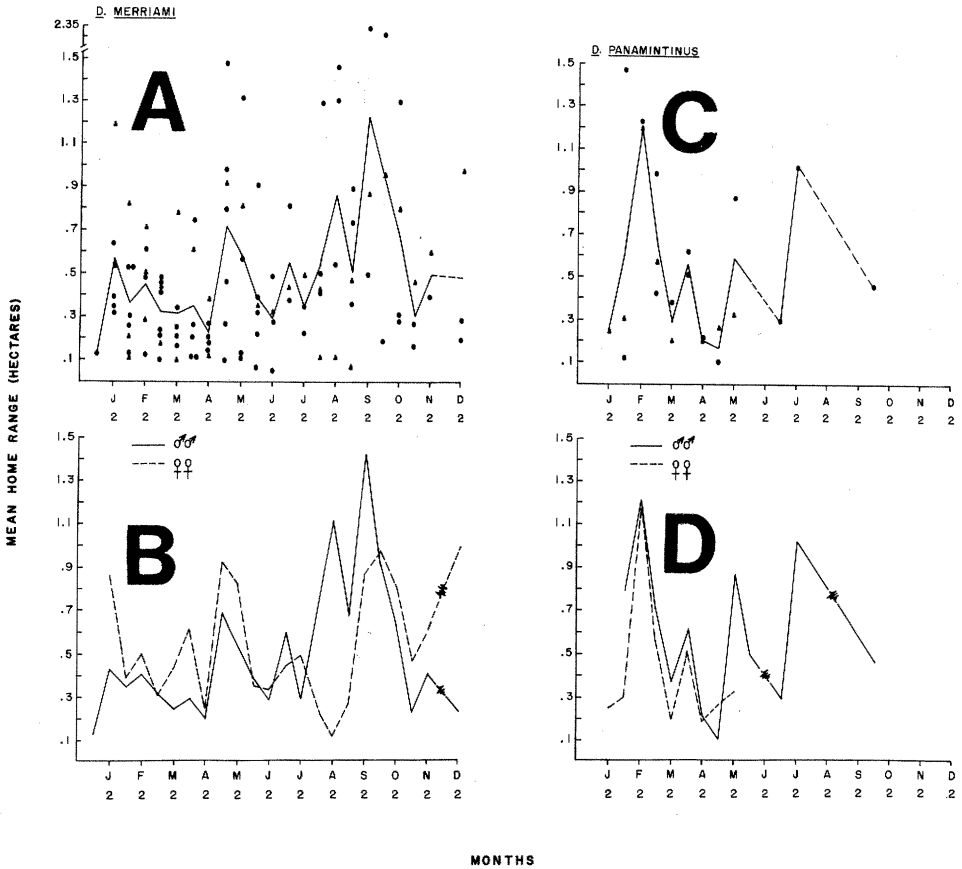


FIG. 2.—Home range estimates (95% probability ellipses) for *Dipodomys merriami* and *Dipodomys panamintinus*. In the upper figures, the lines connect mean values for combined sexes. Circles = males; triangles = females; broken lines indicate no data for that trapping period.

individual in each trapping period that has the largest or smallest home range. When the data permitted, I plotted home range for each individual through the year and found that in all instances the oscillations from week to week were far more pronounced than that shown for mean values.

Using the runs test above and below the median it was determined that males tended towards significantly larger home ranges in the fall (Fig. 2B). Fluctuations in female home ranges did not deviate from randomness. Even so, the female peaks in

TABLE 1.—The proportions of home range estimates based on the frequency of recaptures. Values are given as percentages. Values listed as ≥ 10 recaptures are a percentage of those > 6 .

Species	≥ 10	≥ 6	< 6
<i>Perognathus longimembris</i>	24	56	44
<i>Microdipodops megacephalus</i>	—	39	61
<i>Dipodomys merriami</i>	19	54	46
<i>Dipodomys ordii</i>	—	30	70
<i>Dipodomys panamintinus</i>	4	52	48
<i>Dipodomys microps</i>	18	41	59
<i>Peromyscus maniculatus</i>	46	75	25

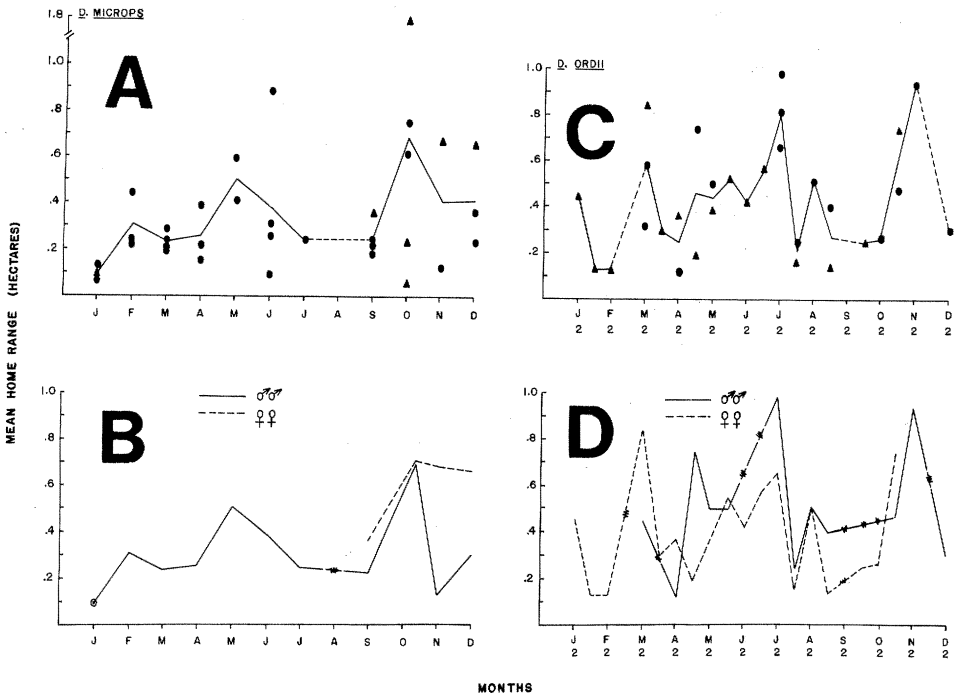


FIG. 3.—Home range estimates (95% probability ellipses) for *Dipodomys microps* and *Dipodomys ordii*. See Fig. 2 for further explanation.

mid-winter, late spring, and mid-fall may reflect changing energy demands and associated foraging ranges. A Wilcoxon sign rank test revealed no significant difference between mean male and female home ranges for the year. Males were in reproductive condition from February to July when range size tended to be depressed. Females showed a similar pattern with only one individual actually showing signs of early pregnancy in June. The increase in home range size exhibited in September corresponded with molt in both sexes.

Dipodomys panamintinus was not abundant on the study site and in fact disappeared for a portion of the year (Fig. 2C and D). Although monthly fluctuations were similar to those of *D. merriami*, the peaks were asynchronous. Individual variation on a given date does not appear to be as marked as in *D. merriami*, and there was no significant difference between males and females. Males were reproductively active from January through May, but only one female showed signs of estrus in April. No trends are apparent with regard to reproductive activity and range size (Fig. 2C and D).

The sexual composition of *D. microps* was unusual in that females were absent from the latter half of January until the first half of September (Fig. 3B). The females that established residency in the study area were subadults and may have exhibited higher than normal movements while in the process of homesite selection. Captures for this species were infrequent during July and August, which may reflect an intolerance of this species to high temperatures (O'Farrell, 1974). There was a trend toward increased home range sizes in the spring and again in the fall similar to that of *D. merriami* (Figs. 2A and 3A). Males were reproductively active from late fall to early spring with one female showing signs of estrus in early January.

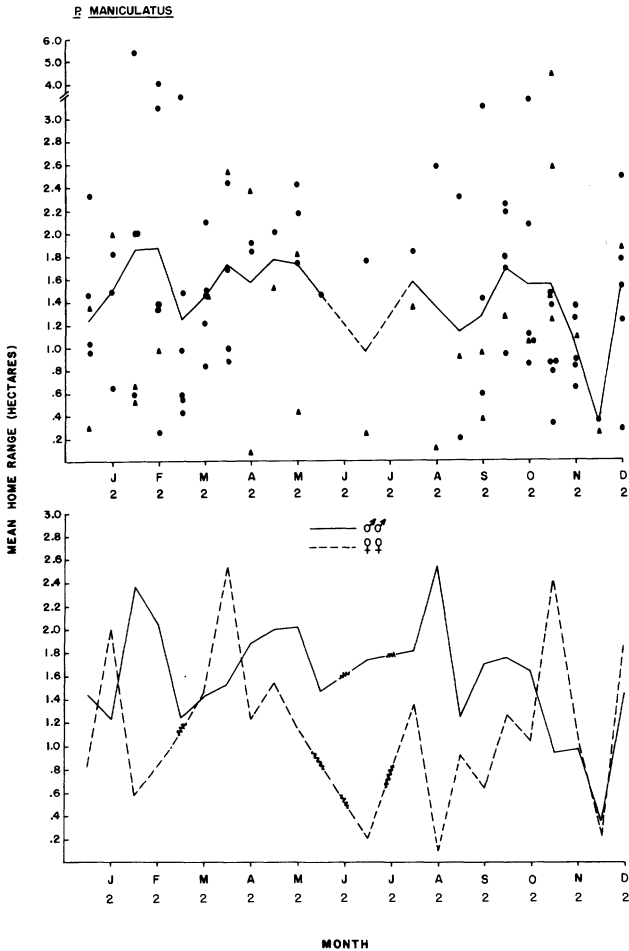


FIG. 4.—Home range estimates (95% probability ellipses) for *Peromyscus maniculatus*. See Fig. 2 for further explanation.

The population of *D. ordii* was small, but recapture data were consistent (Fig. 3C). Home range movements tended to increase through the spring and again in late fall and early winter. There was no significant difference between mean home range sizes of males and females for the year (Fig. 3D). Males of this species exhibited enlarged testes, which were at least partially scrotal throughout the year. Estrus was apparent in early April with signs of pregnancy occurring into May. Two immature *D. ordii* were captured in May and June. Reproductive activity, at least in females, coincided with a reduction in home range size (Fig. 3D).

Home range size for *P. maniculatus* was consistently larger throughout the year than for any other rodent species in the study area (Fig. 4). It should be pointed out that there was a complete population turnover during the summer and that values collected during the latter half of the year are representative of immigrant adults and subadults. Throughout the year, females tended to have significantly smaller home ranges than did males ($P < 0.05$). Females also tended to show peak movements coinciding with reduced male home range size. Also, the spring peak in females coincided with the onset of reproductive activity, with home range declining through pregnancy and lactation.

TABLE 2.—Composite 95% probability home ranges (ha) using both the circular (C) and principal component (PC) methods. N = total number of recapture loci for each species. The ratio of major and minor axes (R) for each composite is also presented as an index of home range shape (1.0 = circular; >1.0 increasing ellipticity). Mean weight (wt) for each species is given in grams.

Species	N	Weight	C	PC	R
Heteromyidae					
<i>Perognathus longimembris</i>	394	8.0	0.46	0.33	2.38
<i>Microdipodops megacephalus</i>	85	12.2	0.52	0.43	1.89
<i>Dipodomys merriami</i>	718	39.8	0.65	0.49	2.21
<i>Dipodomys ordii</i>	172	52.4	0.62	0.43	2.45
<i>Dipodomys microps</i>	233	62.1	0.52	0.45	1.70
<i>Dipodomys panamintinus</i>	132	73.2	0.57	0.43	2.18
Cricetinae					
<i>Reithrodontomys megalotis</i>	13	13.5	1.12	0.95	1.82
<i>Peromyscus maniculatus</i>	509	18.4	1.69	1.42	1.85
<i>Onychomys torridus</i>	29	21.7	1.95	1.34	2.47

Annual composite home ranges allow general comparisons of the nine species of sagebrush rodents (Table 2). The composite value is not a mean value but rather a probability of occurrence area. It was determined by transforming all capture coordinates to deviations from the center of activity, rotating the major axis of each individual home range to a common angle, and then superimposing all the centers of activity. Therefore, a generalized home range estimate is obtained based on all capture points for each species. It is interesting to note in Table 2 that all of the heteromyid rodents demonstrate little or no difference in home range size. Animal size seems to have no effect on range size except for *P. longimembris*. Based on seasons, this species was the most abundant on the study area and high density, rather than small body size, may account for small home range size. It is apparent that *P. maniculatus*, a small cricetine rodent, requires a much larger area than do the heteromyid rodents. Little can be said for home range size for *R. megalotis* and *O. torridus* due to the low number of recaptures recorded for these species.

An attempt was made to examine the relationship between home range size and relative abundance of animals. Correlation coefficients were calculated for home range in relation to total numbers present through time for each species and for total numbers of all species. No significant relationships were observed.

Home Range Shape

In order to examine the general shape of home range, as well as changes in this shape through time, both circular and principal component values were calculated. In addition, the ratio of major and minor axes was obtained as a workable index of shape. As can be seen in Table 2, the circular method of estimating home range size yields a larger value than does the principal component estimate. The composite ratio values also indicate that the shape tends to be more or less elliptical.

An example of changes in shape of home range through the year is presented in Fig. 5; apparent sexual differences during certain times of the year occurred in all species examined. Female range shape was highly elliptical in late summer for *D. merriami*, whereas males of *D. microps* showed this pattern. On the other hand, *D. ordii* females and *D. panamintinus* males exhibited greatly elliptical home ranges in early summer. Home ranges were elliptical in the spring for *P. longimembris* and *M. megacephalus*, but became increasingly more circular during the summer and fall. Home range shape was somewhat elliptical for *P. maniculatus* throughout the year with the ratio fluctuating between 1.5 and 4.0 although major peaks were not observed as in Fig. 5.

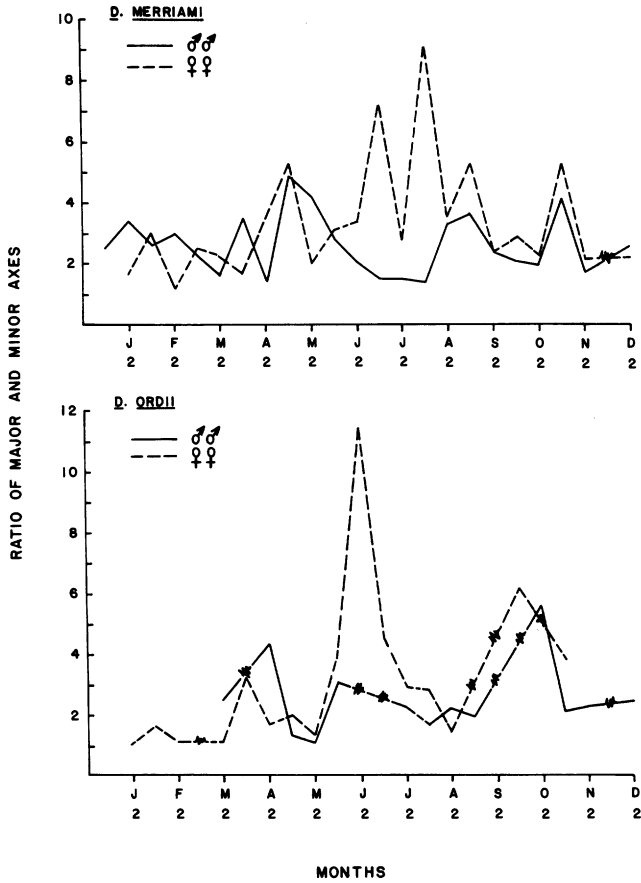


FIG. 5.—The ratio of major and minor axes of home ranges calculated from principal component analysis. A ratio of 1 indicates a circular home range, whereas ratios greater than 1 indicate increasing elliptical shape.

DISCUSSION

The concept of home range and associated movements in mammals has been reviewed and evaluated in detail (Brown, 1966; Jewell, 1966; Sanderson, 1966). When dealing with this concept, most workers utilize Burt's (1943) definition or a modification thereof. These modifications generally consider either temporal and seasonal aspects (Martinsen, 1968; Maza et al., 1973) or social structure (Brown, 1966). As the concept has been expanded, semantic difficulties have arisen. As a result, a number of precise definitions have been advanced which are at best partially restrictive and, therefore, neglect certain aspects of an animal's movements. Many of these definitions are presented in the previously cited reviews and a perusal will verify the confusion and conflict that exists.

While everyone agrees that home range is dynamic in nature, it is generally dealt with in a static manner which reflects the available techniques, data collection, and analysis. Sanderson (1966) describes the techniques utilized for home range study and points out the shortcomings of each. Nocturnal, small mammals are perhaps the most difficult in trying to obtain accurate movement patterns. The most common and still the most practical method of home range determination is capture-mark-recapture. Sanderson (1966) points out that the greatest problem with live-trapping is that an

animal's movements are inhibited while it is within a trap. Because most workers only check their traps once or twice a day, this is indeed a serious problem. In addition, under such trapping regimes sufficient recaptures are obtained for an individual only after an extended period of time. Also, many animals are lost from such calculations because they were not present on the study area for a sufficient length of time. The regimen used in the present study has sought to overcome this problem. By checking traps at 2-h intervals, animals were allowed more time to range freely and sufficient recaptures were obtained for a short period of time. Some individuals were captured five or six times in a single night. Home ranges obtained in this way enable the examination of point-in-time estimates of movements for a greater number of animals, which should allow more biologically meaningful interpretation.

Another difficult problem to deal with is the presence of many grid-edge animals, which yield mainly linear movements. In this study linear movements were not considered. One way to solve this problem is to expand the grid area, which is usually prohibitive due to expense in additional traps and manpower required. I have recently used the present trapping regimen in conjunction with a grid and assessment line configuration (O'Farrell et al., 1977). This method not only gives accurate density estimates but also allows the inclusion of movements beyond the grid border in calculations of home range. The principal component analysis is particularly suited for this type of trapping configuration.

Sanderson (1966) reviews and evaluates the various techniques utilized for analyzing mammal movements and concludes that no method is satisfactory for all situations. He further points out that the quest for home range shape has little significance in itself. I concur that the home range shape is so nebulous due to temporal, spatial, and social factors that further pursuit of absolute demarcation of the area does not justify the effort expended. A square home range is an artifact of grid geometry. It is known that many home ranges conform to either a circular or, more commonly, an ellipsoid configuration (Calhoun and Casby, 1958; Jennrich and Turner, 1969; Mazurkiewicz, 1969, 1971; Metzgar, 1972, 1973; Maza et al., 1973; O'Farrell et al., 1975). I suggest that the nonproductive discourse on true shape of home range be abandoned in favor of the adoption of a standard procedure which would serve as an index of movements but would yield valuable, comparable estimates, which are biologically relevant.

The method which seems best suited is the principle component analysis which was utilized to obtain elliptical areas (Jennrich and Turner, 1969; Mazurkiewicz, 1969). This technique is flexible and allows the analysis of home range configurations ranging from circular to almost linear. It also provides a ready check on the number of animals utilizing only linear movements within the study area for a given point in time. Mazurkiewicz (1971) has pointed out further advantages of this technique, namely the ability to assess the trends toward circularity, and more importantly the orientation of mammal movements in relation to habitat features and coexisting individuals. I will deal with the latter topic in another paper on spatial relationships. In addition, the composite home range for a species (see Results) can be calculated on a monthly, seasonal, or yearly basis. Due to the method of calculation, it yields a probability area which may yield a more useful estimate of home range movements than simple arithmetic means.

The home range estimates in the present study are not comparable with a number of published studies due to differences in methodology and analysis. These will be mentioned in the following discussion. Seasonal changes in home range size as well as annual composite estimates for *Microdipodops megacephalus* are presented in Fig. 1A and B and Table 2, respectively. The only data presented on movements of this species have been given as maximum linear distance traveled (Hall, 1946; Ghiselin, 1969). Ghiselin showed males to exhibit longer movements which correspond to the larger home ranges of males in the summer and fall (Fig. 1B).

Perognathus longimembris was the smallest and most abundant rodent on the study area and showed the smallest annual composite home range of all the rodents examined (Table 2). This species is capable of greater movements as demonstrated during the fall (Fig. 1C and D). This increase may be the result of decreased population pressure and/or a seasonal reflection of food availability. Allred and Beck (1963), Chew and Butterworth (1964), Ghiselin (1969), and Kenagy (1973) present ranges for *P. longimembris* as greatest distance moved. Comparative home range areas can be calculated from 95% radius (Jorgensen and Hayward, 1965; Maza et al., 1973). Their values tend to be higher than those in the present study (Table 2; Fig. 1C). This discrepancy may be due to geographic and social differences but most likely reflects the tendency of this species to have elongate home ranges (Table 2), which would yield inflated circular values.

The movements of *Dipodomys merriami* have been examined in a variety of habitats and geographic localities, although the lack of a standardized approach makes comparison and interpretation difficult. Maximum distances traveled are given by Allred and Beck (1963), Ghiselin (1969), and Kenagy (1973). The values given in other studies (York, 1949; Reynolds, 1960; Chew and Butterworth, 1964; Jorgensen and Hayward, 1965; Maza et al., 1973) present home ranges at the upper end of those found in the present study (Fig. 2A). The trend towards elongated movements for this species (Table 2) may account for these differences. Also, the presence of three larger congeners may have tended to suppress movements. Previous workers noticed larger male home ranges (York, 1949; Reynolds, 1960; Jorgensen and Hayward, 1965), which corresponds to late-summer early-fall trends observed in this study (Fig. 2B), although no significant consistent annual pattern was observed. It is apparent that sexual fluctuations are at least time dependent.

Movement data for *D. ordii* are limited to maximum distance traveled (Ghiselin, 1969) and circular 95% probability areas (Jorgensen and Hayward, 1965; Garner, 1974). The latter values generally fit within the observed variation of home range size in the Reno study area (Fig. 3C). Females have previously been shown to exhibit larger mean home ranges than males (Jorgensen and Hayward, 1965; Garner, 1974), which was not apparent on an annual basis for the present study. Females did possess larger home ranges in the early spring but exhibited decreased range of movements with the onset of reproductive activity (Fig. 3D).

Due to the population structure on the Reno grid, mainly male movements were obtained for *D. microps* (Fig. 3A and B). Female movements were for subadults in the process of establishing new ranges and, therefore, may not be representative of adult females of this species. Maximum distances traveled by *D. microps* are presented by Allred and Beck (1963), Ghiselin (1969), and Kenagy (1973). Males in both studies showed longer movements than females. Mean home range areas based on 95% radii (Jorgensen and Hayward, 1965; Maza et al., 1973) are equivalent to the highest values calculated in the present study (Fig. 3A). The previous values also indicate greater home ranges than for females. The smaller home ranges in the present study may reflect the restriction of this species to shadscale habitat (O'Farrell, 1973).

On the basis of limited data, *Onychomys torridus* demonstrated the ability to regularly move over large areas (Table 2), which is probably related to their predatory feeding habits (Bailey and Sperry, 1929). Maximum distances moved tend to support this conclusion (Allred and Beck, 1963; Ghiselin, 1969). Calculated home ranges based on 95% radii (Jorgensen and Hayward, 1965) yields values approximating 6 ha. These circular areas are probably overestimates inasmuch as *O. torridus* exhibits elliptical movement configurations (Table 2).

The home range and movements of *Peromyscus maniculatus* have been summarized by Stickel (1968) for a wide variety of geographic localities. Data for desert regions

are the least abundant. Maximum distances traveled are presented by Broadbooks (1961), Allred and Beck (1963), and Ghiselin (1969); males exhibited longer movements than females. Jorgensen and Hayward (1965) give 95% radii, which yield home range areas of 2.8 and 2.0 ha for males and females, respectively. These values are well within the range observed for *P. maniculatus* on the Reno grid and are quite large for a small rodent. It appears that in a desert habitat, this species maintains a large home range possibly due to a scattered distribution of food.

As pointed out previously, the lack of a standardized approach makes comparison between different populations difficult at best. The approach taken in the present study suggests a method to systematically examine temporal, sexual, reproductive, density, habitat, and climatic influence on small mammal movements. Home range needs to be examined for each species in habitats with various combinations of species. Home ranges may vary greatly when fewer potential competitors are sympatric.

A static home range value for a particular species, in itself, is not important. The description of the dynamic nature as well as the temporal trends that exist in small mammal movements will allow the determination of abiotic and biotic influence on these movements. This information may then result in the formation of generalized, useful models.

The studies of energetics by Kenagy (1973) and Soholt (1973) present excellent budgets for heteromyid rodents. However, surface activity (in hours) or linear distance were the only criteria used. An animal active for 4 h and ranging over 1 ha should be expending more energy than one ranging over 0.3 ha during the same time period. A knowledge of area traversed at distinct points in time is critical to an examination of time and energy budgets.

ACKNOWLEDGMENTS

I wish to gratefully thank Dr. Arthur C. Risser who provided many helpful suggestions and assistance, enormous encouragement, and long hours of fruitful discussion. Drs. Donald W. Kaufman, Robert M'Closkey, and Bernardo G. Maza reviewed the manuscript. Dr. Frits Went kindly allowed the use of a Desert Research Institute field vehicle. During various portions of the study, I was provided with the able field assistance of Dale Lundahl, Michael Branscum, Joseph Stackpole, Andrew Blaustein, Glen Contreras, and David Koch. I also wish to thank George Campbell of North American Aviation who granted me access to the Warm Springs Valley study area.

This is a portion of a dissertation submitted in partial fulfillment for the degree of Doctor of Philosophy at the University of Nevada, Reno. The study was supported by a grant from the University of Nevada Research Advisory Board.

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Zoological Society of Nevada, P.O. Box 4036, Las Vegas, Nevada 89106. Submitted 8 December 1977. Accepted 7 April 1978.