ANALYSIS OF MOVEMENT PATTERNS IN A

POPULATION OF DIPODOMYS ORDII

by

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CHAPTER I

INTRODUCTION

Population studies are useful in providing an estimate of biological productivity (Andrzejewski, 1967) and dispersal capacity, and thus, gene flow (Blair, 1953). Analysis of patterns of movement within a population of small mammals may reveal factors that influence daily and seasonal activities. Temporal change in pattern of movement by individual animals has been attributed to age (Dice and Howard, 1951), reproductive cycle and food availability (Martinsen, 1968), and changes in density (Stickel, 1960). Sanderson (1966) reviews techniques for quantification of movement data.

My study was conducted to correlate movements of the kangaroo rat, *Dipodomys ordii*, with intrinsic population dynamics and climatic factors. Data accumulated for 15 months from a capture-mark-release study provided a basis for comparison of subunits of the population during different periods of time. These subunits or segments of the population were based on animals grouped by sex, age, and breeding condition. Factors effecting dispersal were analyzed. This type of movement was compared with other kinds of movements by the population.

CHAPTER II

MATERIALS AND METHODS

A live-trapping study was begun approximately 12 miles northeast of Littlefield, Lamb County, Texas (3600 feet) on the Halsell Ranch. Trapping was initiated 11 November 1967 and terminated on 29 February 1969. Soils in this vicinity are Tivoli and Brownfield fine sands, and the area is generally termed a Sandy Land range site (United States Department of Agriculture, 1962). The grid (9.48 acres) contained 18 x 13 trap stations with traps 45 feet apart.

At the initiation of the study, a weather station was established on the northeast edge of the study area. Temperature at ground level (Tempscribe S-730), relative humidity at ground level (Serdex 22-7078), and barometric pressure (Taylor Barograph) were recorded for the first 12 months. Supplemental data were obtained from recordings by the United States Weather Bureau at Littlefield.

VEGETATION.--Two level areas with predominantly mid- and short-grasses were on the area of study. Tall grasses were most abundant on two sloping areas. The vegetation was least abundant during the winter of 1967. Both grasses and weedy species increased through the spring and summer of 1968. Major components of the vegetation as determined by line intercept analysis were: little blue stem, *Andropogon scoparius*, (14.3%); blue grama, *Bouteloua gracilis*, (36.2%); sand sagebrush, Artemisia filifolia, (9.4%); yucca, Yucca campestris, (8.0%), and side-oats grama, Bouteloua curtipendula, (6.5%). It was estimated that 54.3 per cent of the vegetation occurring on the site were climax species (see United States Department of Agriculture, 1962:34).

CLIMATE.--Normal mean annual rainfall in this region is 18.91 inches. June through September of 1967 was characterized by below normal temperatures and above normal rainfall. A total of 20.58 inches of precipitation was recorded in 1968 at Littlefield. Precipitation during the study was above normal, and moisture was unevenly distributed in time. The normal monthly rainfall during July and August is between 1.5 and 2.0 inches. During the warmest period of the study (June through August), 12.32 inches of rainfall were recorded. Temperature means and ranges for each month of the study are shown in Figure 1.

TRAPPING PROCEDURE.--Ninety-six traps were set for three nights every two weeks. No traps were set in January, 1969. Although the formal study was terminated, additional trapping was conducted in March, 1969. Time of sampling was uniform, but alternate halves of the grid were trapped during inclement weather. Trapping sites were rotated in a manner similar to that used by Brant (1962), and a complete rotation of sites occurred each month. Traps used were modifications of the type described by Fitch (1950).

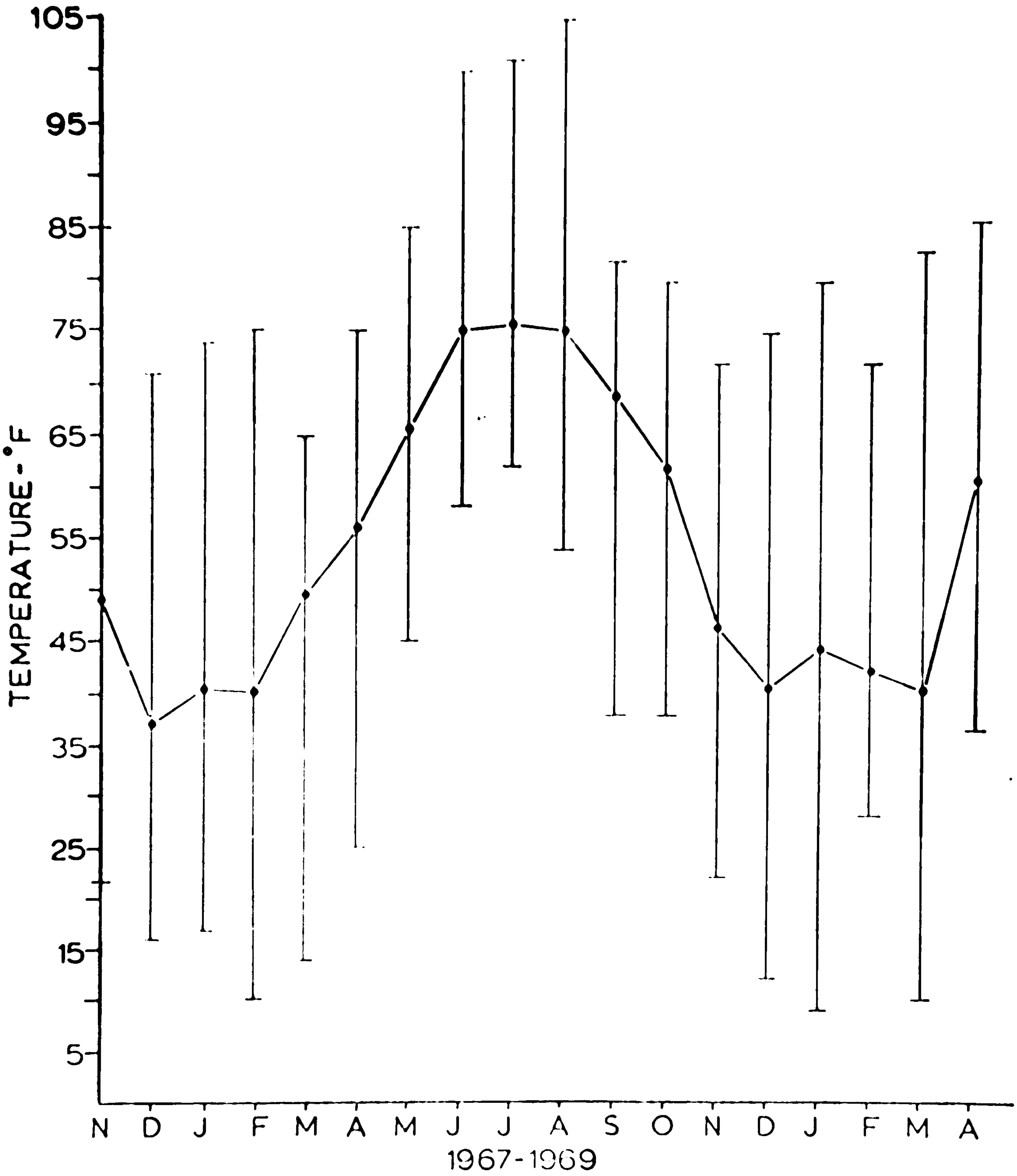

Figure 1. Monthly mean and range of temperatures on the study area from November, 1967 through April, 1969.

A mixture of milo, cracked corn, and rolled oats was used for bait. Newly-captured animals were marked by clipping toes (see Fitch, 1952), and examined for sex, age, and reproductive condition. Animals were weighed in grams with a 250 gram Ohaus spring scale and released at the site of capture.

MEASUREMENTS.--Four indices of movement were measured. Average distance traveled between successive capture points (av. D of Brant, 1962 and see Davis, 1953), maximum distance traveled between successive capture points (av. M of Brant, 1962), and Stickel's (1954) adjusted range length (ARL) were computed for each animal. Another index used was life-adjusted range length, the adjusted maximum distance moved during the course of the study. This measurement permitted comparison of movements of *D. ordii* with range lengths of other species. Individual values were averaged for each species.

STATISTICAL TREATMENT.--Student's *t*-test and a modification of Duncan's Multiple Range Test (Steel and Torrie, 1960) were applied to movement data. The five per cent confidence level was selected for significance in all statistical tests. The study was divided arbitrarily into four periods for analysis. These periods (see Table 2) corresponded with seasonal changes in climate, breeding activity of kangaroo rats, and activity rhythms of associated species. Each measurement (see above) was computed for each animal present in each period. A *t*-test was used to compare the means of each measurement for adults of each sex, two age classes, and the sex classes within the juvenile group for each period.

AGE CATEGORIES.--Maximum body weight of individual kangaroo rats is reached after adult body proportions are attained (Desha, 1967). Body weight was used to distinguish adult from immature animals. Males weighing less than 55 grams and females less than 50 grams were designated as immature (see McCulloch, 1961).

POPULATION DENSITIES.--Total numbers of animals known to occur on the area were used to calculate a minimum estimate of population density. Some animals probably avoided traps, and all marked animals were not taken each month. Resident, immigrant, transient, and young animals were probably sampled in proportion to their actual occurrence. Male and female abundance was figured separately each month.

Traps actually sampled a much larger area than that encompassed by the grid. A strip equal to one-half the width of the average home range is usually added to peripheral trap lines (Blair, 1941). I added, instead, a boundary strip of width equal to av. D for the population in each period (see Brant, 1962). Therefore, sampled area was related to the changes in range of movement of kangaroo rats. In times of peak movement the sampled area was almost twice (17.48 acres) the actual size of the grid.

CHAPTER III

RESULTS

A total of 3174 captures of eight species of rodents were obtained in 5255 trap-nights. Data on movement were computed for 2518 captures of 325 kangaroo rats. Only individuals captured two or more times were used in subsequent statistical tests; these totaled 215. Some mice could have been considered non-residents (see McCarley, 1958 for definition) or otherwise eliminated from consideration if taken only in peripheral traps. However, these were included in the analysis. Those mice captured two times included 31 males and 18 females. Two males and two females were captured 43 and 27 times, respectively.

MOVEMENT.--No significant differences in seasonal movements were indicated between sex or age classes (see Tables 1 and 2). The variances of ARL for adult males and females did not differ significantly in period II; all measurements showed similar variances for these categories in period III. Females of both age classes and juveniles as a group showed the greater degree of variance within each grouping.

On the basis of the above findings, all data for the species were pooled. Analysis of variance for the four time periods was performed. Only population means of av. D and av. M were notably distinct (see Table 3).

TABLE 1

STUDENT'S t-TEST APPLIED TO MOVEMENT INDICES (FT.)

FOR MALE VERSUS FEMALE ADULTS

Period	(N) ♂♂	(N) ♀♀	av. D[!] ♂♂		av. D[!] ♀♀	av. M[!] ♂♂		av. M[!] ♀♀	ARL[!] ♂♂		ARL[!] ♀♀
I Nov.-Feb. 1967-68	(47)	(28)	101.5	*	134.2	129.6	*	161.4	185.1	*	231.3
II Mar.-June 1968	(29)	(37)	85.2	*	73.1	123.8	*	101.7	169.4		162.1
III July-Oct. 1968	(46)	(45)	60.0		63.9	78.9		77.6	135.4		135.0
IV Nov.-Feb. 1968-69	(40)	(35)	68.1	*	92.7	80.4	*	104.4	136.2	*	160.7

(!) = all differences nonsignificant at $P < .05$
(*) = variances significantly different

TABLE 2

STUDENT'S *t*-TEST APPLIED TO MOVEMENT INDICES (FT.)

FOR ADULTS VERSUS JUVENILES

Period	(N)		av. D!		av. M!		ARL!	
	A	J	A	J	A	J	A	J
I Nov.-Feb. 1967-68	--	--	--	--	--	--	--	--
II Mar.-June 1968	(66)	(46)	78.39 *	108.91	111.40 *	138.6	165.27 *	199.03
III July-Oct. 1968	(91)	(20)	61.97 *	74.81	78.28 *	95.74	135.23 *	159.40
IV Nov.-Feb. 1968-69	--	--	--	--	--	--	--	--

(!) = all differences nonsignificant at $P < .05$
(*) = variances significantly different

TABLE 3

ANALYSIS OF VARIANCE FOR THREE MOVEMENT INDICES FOR

DIPODOMYS ORDII (NOVEMBER, 1967-FEBRUARY, 1969)

av. D	av. M	ARL
CV = 69.9%	CV = 80.7%	CV = 56.4%
F = 51.42*	F = 8.85*	F = 8.30

(*) indicates significant at P .05

TABLE 4

DUNCAN'S MULTIPLE RANGE TEST FOR TWO

MOVEMENT INDICES OF D. ORDII

av. D	av. M
III IV II I	III IV II I

Coefficients of variation, as presented, are useful only when compared to values from equivalent studies with similar design and statistical treatment. Presented in Table 4 are results of an application of Duncan's Multiple Range Test to population means of av. D and av. M. Periods are ranked according to size of the mean for each measurement. Lines beneath any two periods indicate lack of significant difference between the values for these periods. Period I differed from all other periods in av. D, while period II differed significantly from period III for this index. Periods I and II were distinguished from periods III and IV in mean values of av. M.

POPULATION DENSITIES AND RATIOS.--Population levels increased through periods I and II and decreased markedly in period III (see Figure 2). Densities ranged from 2.5 kangaroo rats per acre in January, 1968 to 8.7 per acre in July, 1968. A net increase was observed for the year, when equivalent periods I and IV were compared.

Young *D. ordii* may comprise as much as one-half of a summer population (see Desha, 1967). In my study, young animals were caught in greater numbers during March through June. Data indicate that immature animals were added continuously to the population, since juveniles comprised about 11.6, 41.0, 17.3, and 21.0 per cent of the population in periods I, II, III, and IV, respectively. Population peaks and declines were largely functions of successive

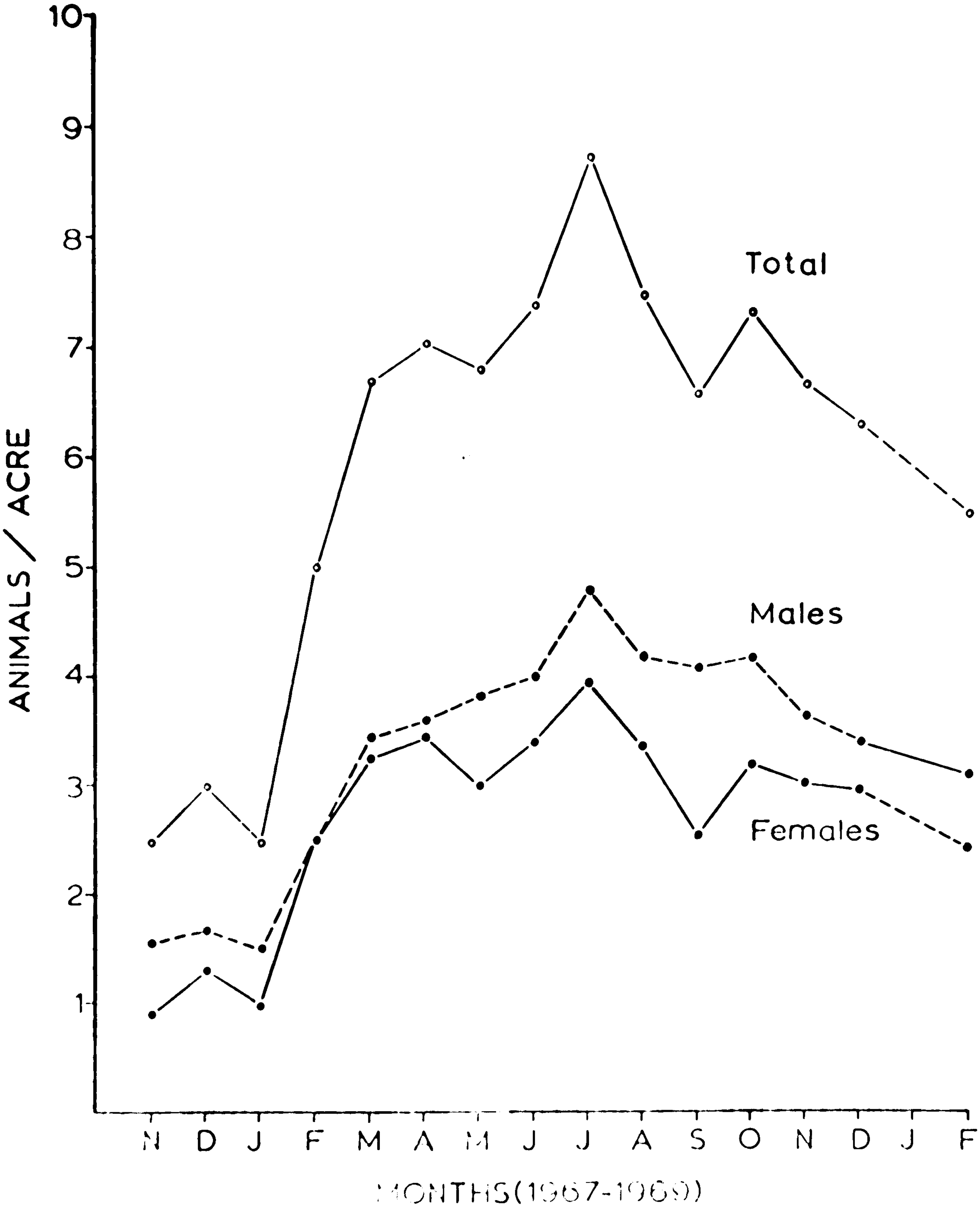

Figure 2. Population densities of D. ordii on the study area from November, 1967 through February, 1969.

increments and losses of young. Johnson (1956) indicated that 40 per cent of kangaroo rat births occurred in March and April. If the gestation period is about 28-30 days (Day et al., 1956), then the several peaks shown in Figure 2 may represent successive additions of young to the population.

Blair (1943) found twice as many males as females in a population of D. ordii in New Mexico. He also reported an instance where females were more abundant than males, and suggested that local fluctuations in sex ratio could occur. My data revealed more males than females in all months except February, 1968. The greatest difference in sex ratio was 1.3 males to 1.0 females in period III. Although sampling error due to differential activity patterns may have occurred, results show a rapid decrease in numbers of females in late summer (see Figure 2).

ACTIVITY.--All monthly trapping records were combined, and total activity was expressed as numbers of captures per 100 trap-nights (see Figure 3). The results showed that population density increased during the study; thus, the overall level of the graph was adjusted upward.

Breeding activity of the population was similar to that reported for the species in Hemphill County, Texas by McCulloch and Inglis (1961). Between 25 and 53 per cent of adult females on my study area showed evidence of swollen vulvas from November, 1967 through March, 1968.

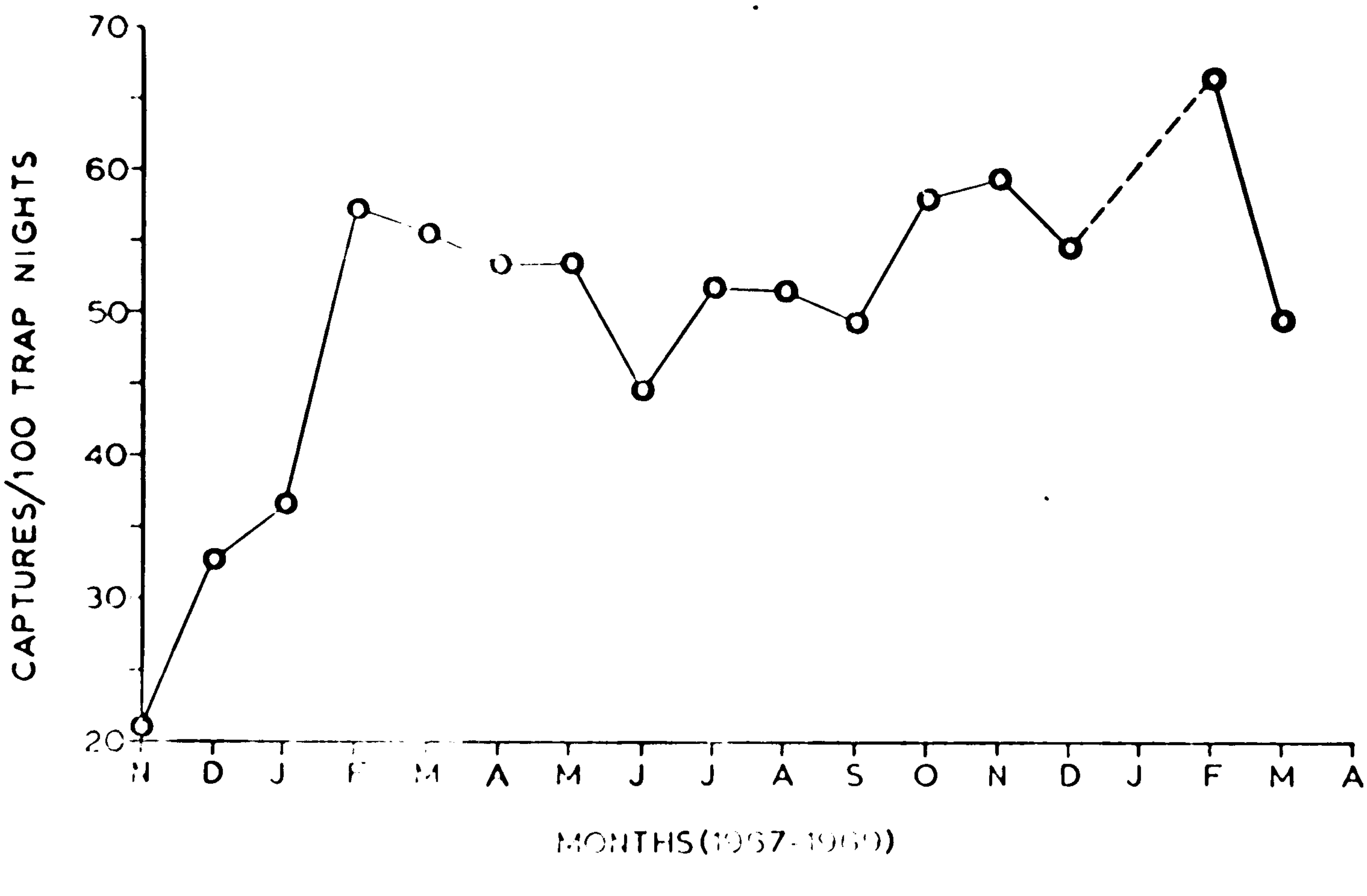

Figure 3. Index of monthly activity of *D. ordii* expressed as captures per 100 trap-nights from November, 1967 through March, 1969.

Reproductive activity was resumed in late September and continued to a peak in late December. Foraging activity appears largely governed by temperature (compare Figures 1 and 3). Total activity declined during period III, a time of peak population density.

OTHER SPECIES.--*Dipodomys ordii* was the most abundant mammal in the area. Three other species, northern grasshopper mice, *Onychomys leucogaster*; plains pocket mice, *Perognathus flavescens*; and spotted ground squirrels, *Spermophilus spilosoma*, were captured enough to provide comparative data. *Perognathus* were the second most abundant small mammals. These four most numerous species revealed average values for life-adjusted range length which were almost the inverse to the order of their abundance (see Table 5). Both age and sex classes have been combined for each species. Interestingly, the average range length of *Onychomys*, primarily insectivorous, differed little from that of the granivore, *Dipodomys*. The value given for *Neotoma micropus* represents a true dispersal movement onto the grid from a nest at the weather station.

Dipodomys and *Onychomys* were the only species appearing in traps every month. Adjusted range lengths for each species varied considerably in each time period (see Figure 4). Again, it is of interest that range of movement varied inversely in periods II and III to apparent population densities of the four species. Magnitude of

TABLE 5

LIFE-ADJUSTED RANGE LENGTHS OF ASSOCIATED SPECIES FROM NOVEMBER, 1967-FEBRUARY, 1969

Species-(N)	Avg. Life Adjusted Range Length (ft.)
Spermophilus spilosoma (12)	321.3
Onychomys leucogaster (43)	221.1
Dipodomys ordii (237)	210.38
Perognathus flavescens (58)	166.6
Neotoma micropus (2)	562.5
Reithrodontomys montanus (2)	283.9
Sigmodon hispidus (1 female)	146.0

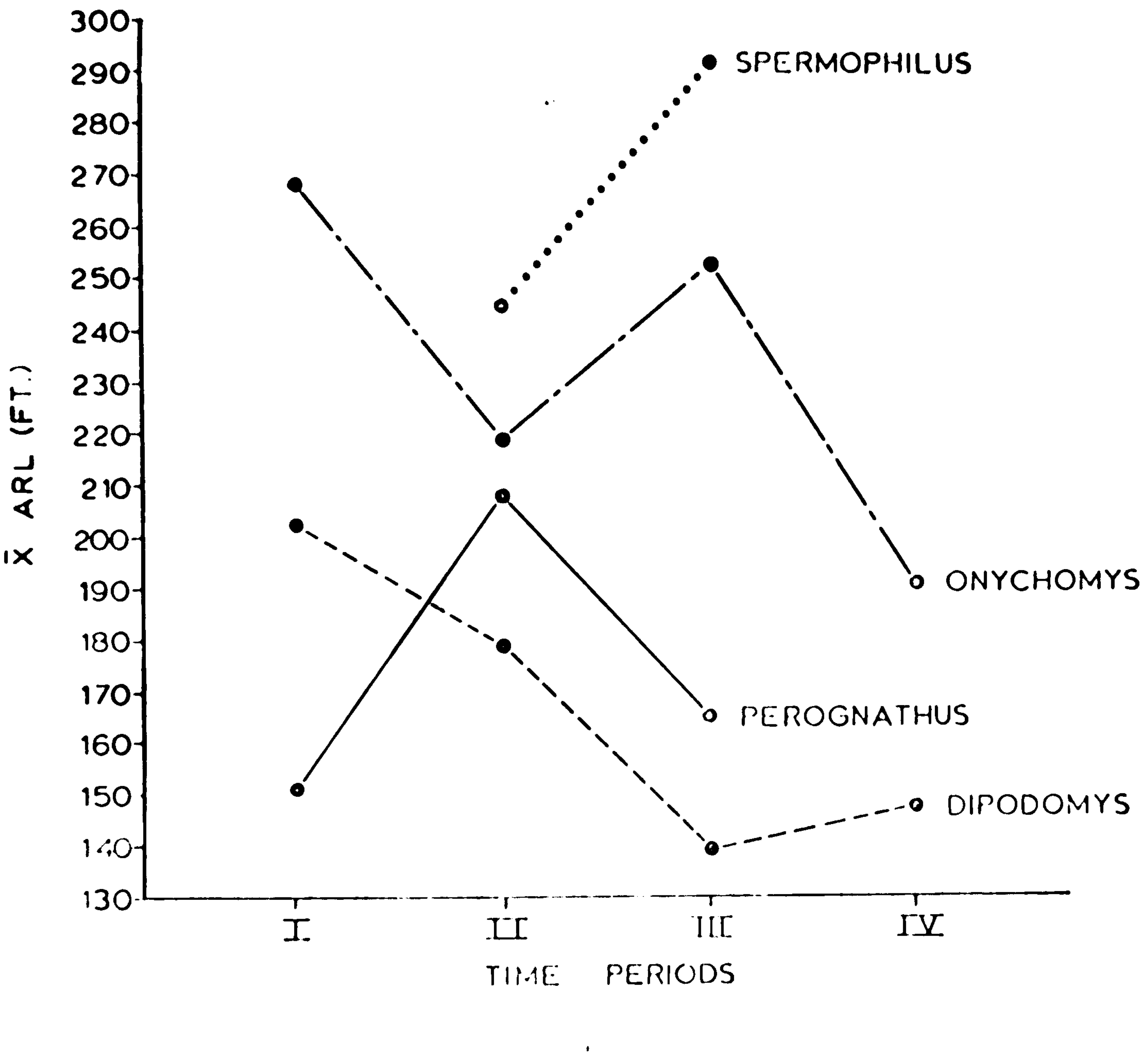

Figure 4. Mean adjusted range lengths for associated species of rodents on the study area in each time period.

movements increased and decreased with overall activity (*Spermophilus*), change in abundance of insects (*Onychomys*), and breeding activity (*Perognathus*).

CHAPTER IV

DISCUSSION AND CONCLUSIONS

Although some animals became prone to enter traps, rotation of trapping sites was thought to have reduced the localization of an otherwise diffuse population (Chitty, 1937). Response of animals to trapping technique and weather conditions must be considered in population estimates (Getz, 1961). Accurate estimates of both population levels and activity probably were obtained in the present study. For example, the time of greatest density was identical to months of reduced activity.

Analysis of movement patterns of a population of *D. ordii* revealed no significant differences between age or sex classes, although temporal variation in pattern occurred. Values of av. D, av. M, and ARL decreased sharply from period I through period III, and an insignificant increase was noted in the final period. Distances traveled were reduced in the population as cover, food, and density increased. Stickel (1960) showed that size of home range in *Peromyscus* diminished as the population increased. Similarly, Bendell (1959) found a decrease in movements with increased density in a population of *P. leucopus* which had been supplied with food.

Average D appears least influenced by previous captures and is easily treated independently for any given time period (Brant, 1962). This measurement was used successfully as an index for size of home range of *Peromyscus leucopus* (Wolfe, 1968). Average M is a more complex function of movement (Brant, 1962) and is not wholly definable at present. In *D. ordii*, successively larger areas were occupied with the onset of breeding and appearance of young.

As a measure of stability of pattern, av. M is comparable in some ways to the increase in size of home range with successive captures. Most previous workers (for example Calhoun and Casby, 1958) have eliminated from analysis those animals with few recaptures or with various numbers of captures in peripheral traps. By eliminating these animals, shifts of movement by the population may be concealed. The home range concept, thus, has been used somewhat erroneously to prove the stability of patterns of movement.

Until recently (see Smith, 1968; French et al., 1968), attempts to quantify dispersal capacity within rodent populations have been based largely on inference. Ingress into a depopulated central plot by *Peromyscus* was attributed to resident animals with established ranges in adjacent areas (Stickel, 1946). Such experiments with reinfestation rates are limited in evaluating dispersal. However, continuous checks of depopulated areas may add important clues. Spencer (1941) found the "drift" of *Dipodomys merriami* to be greatest in winter and lowest in March and April.

While dispersal movement in small mammals is customarily attributed to juvenile animals, young D. ordii do not seem to be more important in dispersal than adults. All species of Dipodomys show a dispersed social organization characterized by adult isolation except in breeding seasons (Eisenberg, 1963). According to Eisenberg, maternal care gradually diminishes; the female may abandon the young at weaning. Siblings may remain together several months. Litter size is decreased in the genus, while gestation period and longevity are increased. Longevity records of 34 months have been reported in natural populations of D. ordii (McCulloch and Inglis, 1961).

In the present study, many multiple captures involving siblings and, presumably, mother and young individuals were obtained. Selection would appear to favor early breeding by the population. Thus, young would be produced and weaned before the appearance of predators such as snakes. Juveniles were more heterogeneous as a group in distances moved, and immature animals showed a markedly disproportionate decrease in av. D to that shown by adults from periods II and III (refer to Table 2). It seems, therefore, that the criteria for dispersal must be unidirectional movement and proven contribution to the reproductive success of the population (see Howard, 1960).

Future work with movement and dispersal should include controlled experimentation with factors determining movements. Jameson (1951) stressed the consideration of habitat preference as the degree of specificity of demands correlated to how well the habitat meets these demands. This approach should be extended to the analysis of movements. If the activity of an animal is determined by rate of metabolism and its structural limitation, then an intrinsic home range size could be a control on the population density (McNab, 1963).

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