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DEMOGRAPHIC AND REPRODUCTIVE PARAMETERS OF THE
YELLOW-CHEEKED POCKET GOPHER
(*PAPPOGEOMYS CASTANOPS*)

MICHAEL J. SMOLEN, HUGH H. GENOWAYS, AND ROBERT J. BAKER

ABSTRACT.—A population of *Pappogeomys castanops simulans* was live-trapped on a 3.5-ha study area in Lubbock, Texas, from September 1971 to September 1973. Seasonal and annual differences in population size were observed, with the population fluctuating between 20 and 25 gophers. Female reproductive activity began in January and continued until October, with an obvious period of recruitment lacking; however, a peak was observed in March and April. Females produced as many as three litters per reproductive season. Females born early in the year were sexually mature within the reproductive season of their birth. Females had an average survival rate of 56 weeks in the trappable population as compared to a 31-week survival rate of males. Neonate through subadult survival of pooled males and females was 72.7%. The gophers had a clumped distribution on the study area, with more mature females forming the centers of the clumps. Subadults of both sexes and adult males were distributed peripheral to adult females. Adult females showed few shifts in their home range configuration whereas adult males and subadults of both sexes had more labile home range configurations. Females arranged their home ranges so as to provide isolation from other gophers. Males, on the other hand, tended to align their home ranges so as to contact more animals, especially mature females. Offspring dispersed from the maternal burrows as juveniles or subadults. Colonization frequently occurred adjacent to the maternal home range, although long distance moves also were observed. Once a home range was established, few shifts were observed.

Pocket gophers (Family Geomyidae) are among the most variable mammals in cranial, exomorphological, and karyotypic features. This variability has long interested mammalogists, and has been manifested in an abundance of research concerning inter- and intraspecific variation. An understanding of the overall population biology associated with this variability can provide valuable insight into the general processes involved in evolution.

Before the effects of the interactions and dynamics that occur among subspecies and species can be understood, however, it is necessary to determine and estimate the demographic parameters that occur within and between populations of the same subspecies. Such studies of geomyid population parameters are primarily restricted to *Thomomys* (Hansen, 1960, 1962; Howard and Childs, 1959; Ingles, 1952; Miller, M. A., 1946; Miller, R. S., 1964; Vaughan, 1962) and *Geomys* (Adams, 1966; Wilks, 1963; Wing, 1960; Wood, 1949) with *Pappogeomys* having received less attention. It is especially important to understand these parameters because *Pappogeomys* can be found contiguously with *Geomys* and *Thomomys*, but it inhabits more xeric areas (Reichman and Baker, 1972) and displays less overall variability in exomorphology and karyology among subspecies and species (Russell, 1969; Berry and Baker, 1972). Studies concerning the population processes are currently limited to assessing movement (Williams and Baker, 1976) and reproductive activity (Ickenberry, 1964).

The aim of this study was to assess the demographic and distributional parameters of a population of *Pappogeomys castanops*. It was hoped that this would provide an insight into the basic population processes of gophers of this genus, and allow comparisons of geomyid life history strategies.

MATERIALS AND METHODS

A population of *Pappogeomys castanops simulans* was trapped from September 1971 to September 1973 on a study site located at the Lubbock Municipal Airport, Lubbock Co., Texas, 988

TABLE 1.—Mean monthly air and soil (45 cm) temperatures and precipitation during the study years (1971–1973). Air temperature and precipitation data were collected by the Department of Commerce, United States Weather Bureau Facility at the Lubbock Municipal Airport. Soil temperature data were collected by the Texas A&M Experimental Station, 3.2 km north of the study site.

Environmental parameters and years	Month											
	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.
Air temperature (°C)												
Average	21.8	16.8	9.2	5.2	3.8	5.7	9.3	15.5	20.4	25.2	26.6	25.7
1971–1972	21.3	16.6	10.4	6.5	5.2	7.7	13.5	18.7	19.7	24.9	24.7	23.6
1972–1973	21.7	15.3	5.8	3.3	1.6	4.6	10.8	12.8	19.9	24.9	25.2	25.4
Soil temperature (°C)												
Average	24.9	18.3	11.8	8.7	6.0	7.1	8.8	15.1	20.8	25.8	28.9	27.8
1971–1972	24.1	19.0	12.8	6.7	5.7	6.7	12.9	17.6	20.6	25.2	25.7	25.5
1972–1973	23.6	20.0	9.6	4.8	3.8	5.0	9.4	12.1	19.8	26.4	28.4	28.5
Precipitation (cm)												
Average	4.5	4.7	1.2	1.1	1.3	1.3	2.2	2.7	7.9	7.4	5.4	4.3
1971–1972	14.0	4.5	1.1	2.1	0.4	0.3	T	0.9	8.1	13.6	11.4	13.7
1972–1973	7.5	4.4	2.5	0.8	3.7	3.2	4.8	3.6	1.1	0.8	10.6	0.9

m. The site was chosen for its accessibility and the presence of a naturally occurring population of gophers.

Vegetation.—The floral composition occurring over the sandy clay loam soils of the entire study area is most unlike the mixed prairie community commonly encountered on the High Plains. Sandbur (*Cenchrus* sp.) was the dominant species over the entire 3.5-ha study area. A few other species of grasses did occur in the area, but were limited to a few isolated patches commonly associated with recent man-caused disturbances. This predominance of sandbur resulted in a general lack of ground cover.

Weather.—Local air temperature and precipitation data were obtained from the United States Department of Commerce Weather Bureau Station, which is located at Lubbock Municipal Airport. Soil temperatures were obtained from the Texas A&M Experimental Station, which is located about 3.2 km north of the study site. The winter and spring of 1972 were drier and warmer than the average (Table 1). Later, a cooling trend developed in June and persisted through the winter of 1973. Accompanying this cooling trend was an increase in monthly precipitation.

Trapping.—A 3.5-ha staked trapping grid was constructed, consisting of 26 rows of 6 stations each, at a row and station interval of 15 m. The grid was designed to include all gophers observed in the area in order to monitor the entire population occurring on the airport property.

The grid was extensively trapped through a 2–3 day period, with the aim of capturing all gophers on the study area. Live-traps (Baker and Williams, 1972) were set in all active burrow systems, as determined by recent mounding activity, and checked repeatedly throughout the day. Traps were spaced, however, to avoid repeated recaptures in the same trapping period. During the first year, the grid was trapped every four weeks. The interval between trapping periods was increased to 90 days during the second year.

Toe clipping was used to identify individuals, with clipping restricted to digits on the hind feet and pollex. Removal of more than two toes was rarely necessary for identification. Sex, toe clips, weight, reproductive and molt characters, and trapping coordinates were recorded for each capture. Reproductive characters included testes position in males, and the presence or absence of vaginal perforation, pubic symphysis position, mammae development, and presence of embryos in females.

RESULTS

Population Size

During the 115 weeks of the study, 48 male and 46 female *Pappogeomys* were trapped a total of 845 times. Mean number of animals known alive and captured per

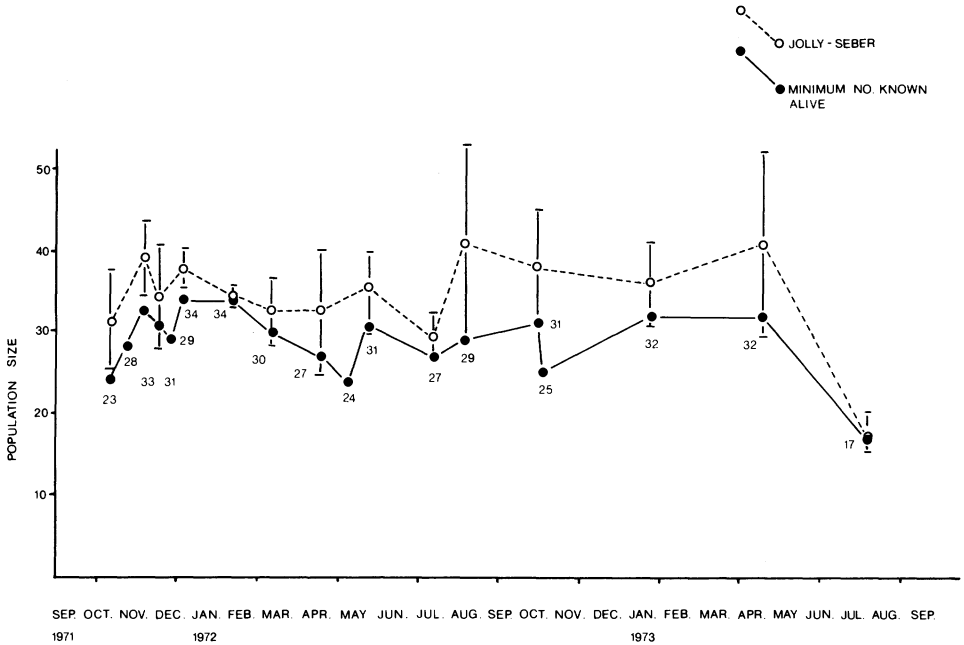


FIG. 1.—Estimates of number of *Pappogeomys castanops* on a 3.5-ha grid in Lubbock, Texas. The numbers immediately below the solid circles are the minimum number known alive. The vertical lines indicate the 95% confidence limits about the Jolly-Seber estimates.

trapping period was not significantly different ($t = 0.01$; $df = 32$) between males ($\bar{X} = 0.65 \pm 0.11$ SE; $n = 17$) and females ($\bar{X} = 0.66 \pm 0.10$; $n = 17$). Furthermore, there was no significant difference ($t = 1.29$; $d.f. = 32$) in the mean proportion of males ($\bar{X} = 0.23 \pm 0.11$; $n = 17$) and females ($\bar{X} = 0.33 \pm 0.12$; $n = 17$) recaptured in the same trapping interval. These data indicate that the trap design and trapping methods were sufficient to sample the population accurately.

The population size on the grid is estimated by the minimum number known alive between intervals, and the Jolly-Seber method (Caughley, 1977). The Jolly-Seber estimates are consistently higher than those determined by minimum number (Fig. 1), although the minimum number estimates usually occur within the 95% confidence limits of the Jolly-Seber estimates. Disparities between the methods, especially March to May 1972 and August 1972 to April 1973, are believed to be due to the combined effects of the gradual lengthening of trapping intervals and the influence of periodic recruitment on the formulas associated with the Jolly-Seber method. Population size as estimated by minimum number is relatively constant throughout the study.

Seasonal and annual differences in population size were observed (Fig. 1). The number of gophers gradually increased from October through January in both years of study. The remaining months, however, deviated between years. After January 1972, the numbers gradually decreased until May, whereas the number of animals remained high during this interval in 1973. The size of the population again decreased from May through July in both years, with the 1973 interval characterized by a more precipitous decline. Despite the observed seasonal changes in number, the population lacked an obvious period of recruitment.

Females in the initial population were in greater proportion than males, with the sex ratio deviating significantly from an expected 1:1 (Fig. 2). However, the January

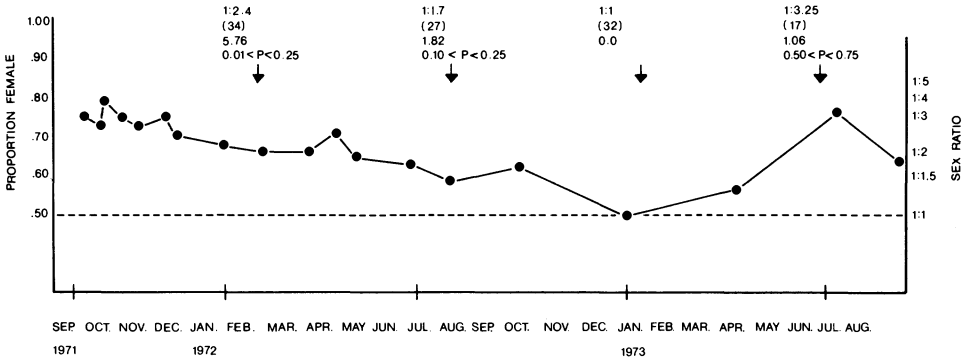


FIG. 2.—Proportion of female *Pappogeomys castanops* in the study population. Sex ratio, sample size (in parentheses), χ^2 value, and probability values appear above the January and July data points.

1973 and both July periods were not significantly different from a 1:1 sex ratio when considered in separate, individual tests.

The initial 3:1 numerical superiority of females slowly declined during the study, and a 1:1 sex ratio was obtained 67 weeks later. The female numerical advantage was quickly re-established, however. Despite these fluctuations, there was no significant difference ($\chi^2 = 4.50$, d.f. = 3) among the sex ratios of the four periods of January and July of both 1972 and 1973.

Reproduction

Age at sexual maturity.—Weight at capture and symphysis resorption were used in the estimates of age at sexual maturity for females. Estimates of the age at sexual maturity of live-trapped males have been shown to be inaccurate because of the lack of a reliable and detectable external change associated with testes development (Hisaw, 1924; Howard and Childs, 1959). Thus, calculations involving both weight and the presence of active molting from juvenile to subadult pelage were applied to males and females in order to estimate male maturity. Only those individuals caught in two successive trapping periods and observed undergoing molting or pubic symphysis resorption were utilized in the calculations. Weight was determined by calculating the mean of the weights in the two trapping periods involved.

The mean weight at sexual maturity of females was slightly higher in the estimates involving symphysis resorption ($\bar{X} = 235.8 \text{ g} \pm 30.2$; n = 6) than in molting ($\bar{X} = 222.0 \text{ g} \pm 19.3$; n = 5). However, despite the apparent close relationship, the time of initiation of both processes is highly variable. One female began post-juvenile molt five weeks prior to symphysis resorption, whereas another began molting and resorption in the same interval. Male estimates were higher than the molt estimates of the females ($\bar{X} = 244.0 \text{ g} \pm 59.6$; n = 5), although the difference is not significant ($t = 1.36$, d.f. = 8). Females weighing less than 230 g and males less than 250 g were considered immature animals in later analyses.

Reproductive activity.—Reproductive activity of females was estimated as the proportion of pregnant and/or lactating individuals in the mature population. Reproductive activity was observed as early as November, and gradually increased to a peak in March and April (Fig. 3). The proportion of active females fluctuated until October when reproductive activity appeared to cease. Although trapping intervals were different between years, and trapping terminated in September 1973, the annual cycle of reproductive activity was similar between years. Females produced multiple litters

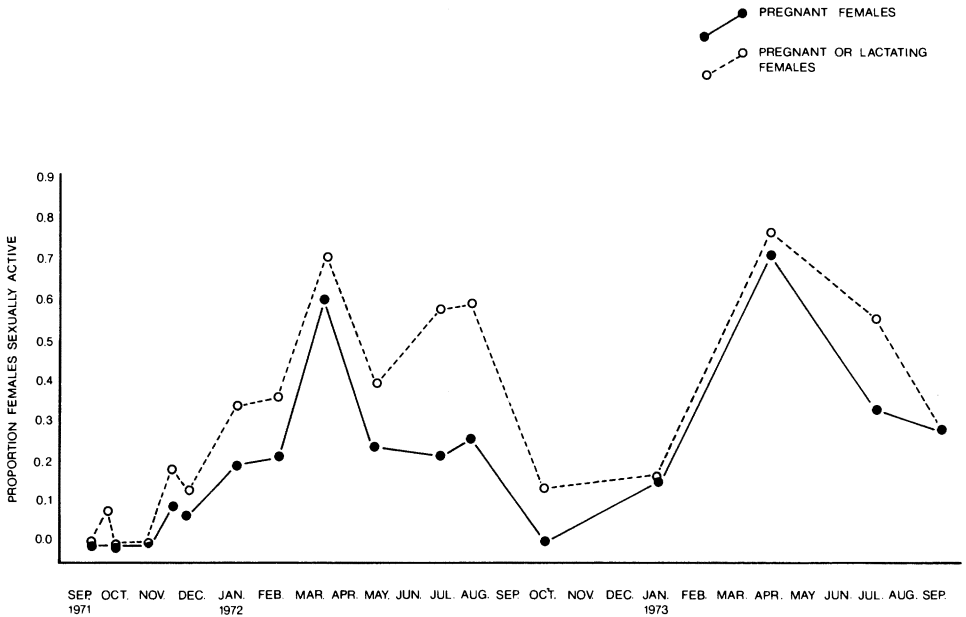


FIG. 3.—Proportion of female *Pappogeomys castanops* pregnant and/or lactating.

through the reproductive season. Three females had a minimum of three litters, and possibly four litters, in one reproductive season. All three were adults and were pregnant in January or February.

Incidences of plural occupancy of a male and a female in a single burrow were observed for the months of January, February, and October. This suggests that males were reproductively active as early as October, and probably remained active until after the March–April female reproductive peak. It is not known when male activity declines, if at all.

Offspring began appearing in the population in April, and continued until October. The mean weight of immature males when first captured was 172.4 g ($n = 17$) with the lowest weight being 90 g. Immature females averaged 170.3 g ($n = 12$) at first capture, with the low weight being 110 g.

Females matured within the reproductive season of their birth, as observed by symphysis resorption and pregnancies. Immature females first captured during the period of December through May were pregnant and lactating by July of the year of their birth. Immature females first captured after May resorbed their pubic symphyses during the summer but none of these females was observed to be pregnant or lactating until the following year.

Survival

Survival rates of offspring from the 1971 and 1972 breeding seasons were estimated from life table analysis as summarized in Caughley (1977). Cohorts consisted of those animals born between March and June of their respective years. The 1971 cohort consisted of those gophers determined to be young of the year and adults in October 1971. Life tables were standardized to the October values of the 1972 cohort to allow comparisons of survival rates between years.

Subadult and early adult survival rates were similar for males and females (Fig. 4). However, in January 1972, the survival rate of males decreased sharply while that of

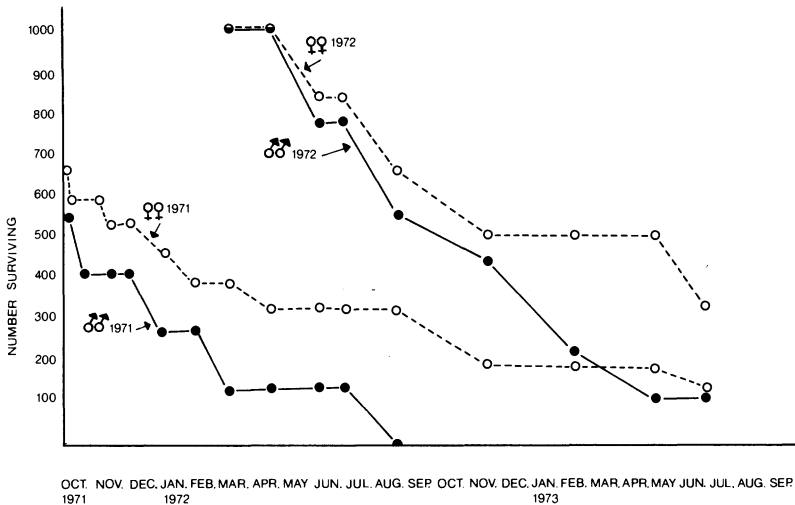


FIG. 4.—Survivorship curves from life table estimates of the survival of the 1971 and 1972 cohorts of *Pappogeomys castanops*.

the females remained unchanged. The cohort in 1971 had an apparent lower survival rate than the 1972 cohort. Females in both cohorts were noticeably longer lived than their respective males. Females in the 1972 cohort had an average survival of 56 weeks in the trappable population, whereas the males averaged only 31 weeks. Furthermore, two females of the 1971 cohort survived 105 weeks, and were still alive at the termination of the study. Males of both cohorts were shorter lived, with the 1971 cohort disappearing in October 1972. One male from the 1972 cohort remained alive in September 1973 (76 weeks), when the study was terminated.

Neonate through subadult survival rates were estimated by comparing the number of expected offspring to the number actually recruited into the population. Twenty females were observed pregnant or lactating during the study. The mean litter size of two pups per litter, as determined by Ickenberry (1964), predicts 44 offspring. Thirty-two gophers were observed to enter the trappable population, a survival rate of 72.7%.

Growth Rates

Comparisons of rates of growth between sexes of subadults were made using regressions of instantaneous growth rates per mean weight (Brody, 1945). Individuals trapped in consecutive periods and whose interval did not exceed 6 weeks were included in the calculations. Intervals were adjusted to produce instantaneous growth rates per 4 weeks.

Slopes of the regression lines for males and females (Fig. 5) were not significantly different ($t = 1.13$; d.f. = 81), indicating that the rates of change in growth were similar between sexes. Analysis of the height of the slopes, however, showed that there is a significant difference between the elevations of the regression lines ($t = 10.65$; d.f. = 82). Although the rates of growth from subadult through adult were similar between sexes, males added significantly more weight per interval of growth than did females of the same age.

Distribution

Home range size.—Home range size was estimated by a modified minimum area method. Capture coordinates were plotted for each gopher that was trapped five or

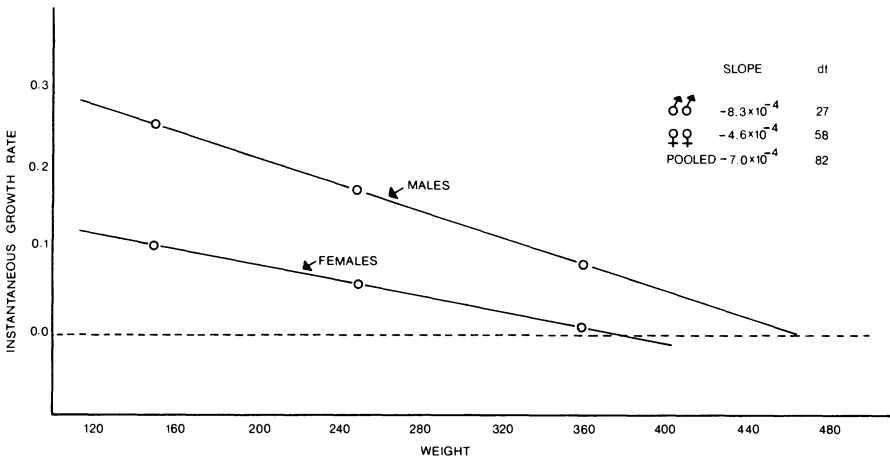


FIG. 5.—Instantaneous growth rates per 4 weeks for male and female *Pappogeomys castanops* in a population from Lubbock, Texas.

more times. The peripheral points were connected, as in the minimum area method (Mohr, 1947; Hayne, 1949), and the longest distance between any two points was determined. Two home ranges were computed for any animal that moved a long distance and did not return to its previous trapping localities. This calculation is not intended as a quantitative analysis of the size of the area a gopher inhabits, but it provides an estimation for use in analysis of movement, density, and distribution.

Mean home range length was greater for males ($\bar{X} = 46.89 \text{ m} \pm 11.46$; $n = 8$) than females ($\bar{X} = 37.05 \text{ m} \pm 5.31$; $n = 25$). Males also displayed a more erratic sequence of moves as indicated by the greater standard error.

Movement.—Five males moved distances greater than 47 m in a single interval. Four of the moves occurred between May and September 1972 when gophers traversed 110.0, 132.2, 195.2, and 127.9 m. The fifth move was shorter (84.1 m) and occurred in January 1973. Four of the animals were mature at the time of the move.

Nine females moved distances greater than 37 m in an interval. Three were subadults and were apparently moving away from their natal burrow systems (46.8, 50.3, and 165.9 m). This is inferred in that two animals were repeatedly trapped within the home range of an adult that was previously lactating, and these moves resulted in establishment of new home ranges. Three moves (49.4, 59.1, and 194.8 m) involved pregnant females. Two were not visibly pregnant in the trapping period prior to their move but were pregnant in the following period. The third was pregnant in the period prior to its move. None returned to its previous home range. Two moved (49.3 and 191.1 m) in apparent response to high density. Both inhabited areas that had two other gophers within 38 m. The ninth female's move of 66.5 m does not fit any of the above situations.

The stability of home ranges differed between sexes. Adult males appeared very mobile and transient with their home ranges frequently modified by short directed moves. Adult females had stronger home range affinities, with few long directional moves observed (Fig. 6).

Movements of juveniles and subadults were more variable. Juveniles appear restricted to their natal burrow systems. Directional moves by subadults were observed away from the natal burrow systems. Colonization and burrow development frequently were in the immediate vicinity of the natal burrow (Fig. 6).

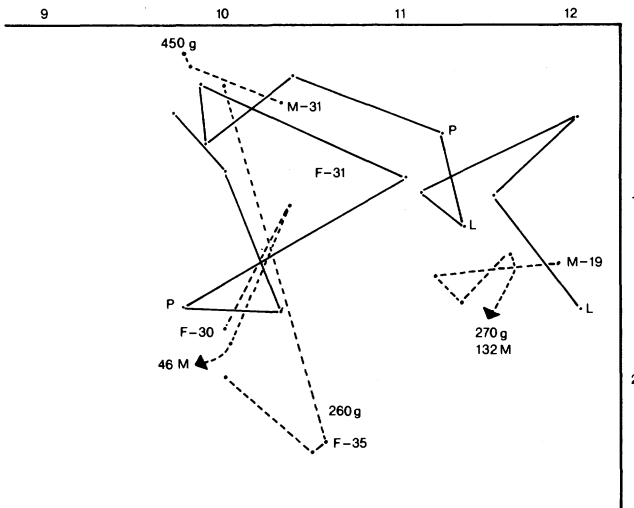


FIG. 6.—Movement of a female *Pappogeomys castanops* (F-11) and her progeny (M-19, M-31, F-30, F-31, and F-35). The numbered axes are the station and row coordinates of the trapping grid, the arrow indicates distance and direction moved to another portion of the grid.

Relationship of distribution.—Poisson distribution analysis was used to determine if home ranges were distributed randomly or clumped. The data were divided into the distributions occurring in the January through July and August through December periods of each study year. The trapping grid was subdivided into 16 squares, 45 m on a side. The frequency of centers of activity in each square of those animals caught four or more times was the basis of the distribution tested.

The distribution of gophers was clumped (pooled $\chi^2 = 13.28$; d.f. = 3; $s^2 = 1.81$; $\bar{X} = 1.32$), with no significant difference among study periods (heterogeneity $\chi^2 = 2.03$; d.f. = 9). Two clumps, which were approximately 136 m apart, were observed throughout the study. Each clump was characterized by the presence of at least two adult females, which comprised the core of the clump and were surrounded by adult males and subadults of both sexes.

Four of the adult females involved entered the trappable population in the core of the clumps, and survived the entire duration of the study at the same location. Individual adult males frequently shifted their home range away from the area surrounding the core of the clumps. Such shifts were of a seasonal nature, with movement away from the core coinciding with the cessation of female reproductive activity.

Density.—Density estimates were made for males and females in January–June and July–December of both years. The coordinates of individuals caught at least four times per analysis period were plotted. The center of activity was calculated and a circle with a radius of the mean of the long axis of the home range was drawn about the activity center of each individual. All mature gophers known to be alive in the area were tallied.

Females inhabited less dense areas than males. The difference is greatest in January–June when the mean density on the male's home range (4.31 ± 0.74 ; $n = 16$) was significantly higher than the density in the home range of females (2.27 ± 0.36 ; $n = 33$). The July–December densities were again higher in males (3.00 ± 0.68 ; $n = 6$) though the difference is not significant from those of females (2.00 ± 0.34 ; $n = 31$). Densities of females remained constant between January and July.

TABLE 2.—Median distance (m) of male to nearest male ($\delta\delta$) and female ($\delta\varphi$), and female to nearest male ($\varphi\delta$) and female ($\varphi\varphi$). Sample sizes are in parentheses. Sexual and seasonal differences are analyzed utilizing Kruskal-Wallis H test, with χ^2 values corrected for ties.

Seasons	$\delta\delta$	$\delta\varphi$	$\varphi\delta$	$\varphi\varphi$	χ^2
September–December 1971	28.18 (9)	13.99 (9)	25.11 (17)	25.39 (19)	5.89
January–July 1972	66.73 (4)	14.85 (4)	32.35 (18)	29.62 (18)	5.54
August–December 1972	21.05 (7)	14.42 (7)	24.02 (16)	22.97 (16)	7.22
January–July 1973	46.57 (2)			31.32 (13)	2.33
χ^2	3.01	4.42	2.08	4.29	

Home ranges of females were more evenly spaced than those of males. Furthermore, females frequently had large buffer strips that provided isolation from other gophers of either sex. This is particularly evident in the analysis of the median distance of nearest male and female (Table 2). Females were consistently 22 to 32 m from the nearest gopher. Males, on the other hand, are situated in closer approximation to females than to other males. Their proximity to other males was highly variable as demonstrated in the greater variability among median distance values in the male-male comparison in Table 2.

DISCUSSION

The combined effects of population size and the behavior of individuals determine the amount of intra- and interpopulation variability in geomyids. Individual parameters such as longevity, fecundity, and vagility determine the amount of genetic diversity and stability within a population. However, the spatial relationships of populations, their degree of isolation, and population sizes determine the amount of genetic variability among populations.

The population of *Pappogeomys* studied is believed to be relatively isolated. Gophers may have inhabited areas adjacent to the grid, although signs of gopher activity in this area were infrequent. A few animals, including some first caught as subadults, vanished from the trappable population, only to be caught again up to 24 weeks later. These animals probably moved off the area, although it is not known whether they moved to another population. Additional animals were first captured as adults, and apparently were immigrants from either another population or the peripheral area. Movements of this nature are important for the maintenance of genetic heterozygosity.

Population size was consistently low throughout the study, unlike some populations of other gopher species that have been studied (Howard and Childs, 1959; Wilks, 1963). Small population size accompanied by a low turnover of individuals in a species with low vagility would promote inbreeding, genetic drift, and an increase in the probability of extinction. Magnitude and rates of these effects upon the population are dependent upon the demographic, reproductive, and vagility parameters of the individuals in the population.

Longevity of gophers is high, with female *Pappogeomys* having an average longevity of 56 weeks, which is comparable to the 55 week longevity of *Thomomys bottae* (Howard and Childs, 1959). Of more importance is the fact that 25% of the females in both cohorts of *Pappogeomys* were still alive 86 weeks after entering the trappable population. These additional weeks allow these females to be active through two March-April peaks in reproduction. Thus, each of these females has the potential to produce from four to six litters in its life as opposed to the three litter potential of those females surviving only 56 weeks.

Males, on the other hand, had a relatively shorter life expectancy than females. The average longevity for both cohorts is 31 weeks, an estimate identical to that found for

male *T. bottae* (Howard and Childs, 1959). This shorter life span means that only about 20 to 25% of the males persist to take part in the reproductive peak of the following year. It is important to note that there is no difference in longevity of either sex between *T. bottae* and *P. castanops*. There are no comparable longevity estimates available for *Geomys*.

Weanling-juvenile survival rates are high. This is probably due to protection offered by both the natal burrow system and the solitary, aggressive female. Mortality, however, is greatly increased as juvenile-subadults move to establish their own burrow systems. Mortality rates were similar in the young adult males and females, but began to diverge with the onset of January reproduction. Female survival rates plateau from January through July or August, whereas male mortality increases sharply. Increased activity associated with breeding may be responsible for the increase in male mortality.

Such life history parameters as length of reproductive season and litter size differ between *P. castanops* and other species of gopher. *T. bottae* (Miller, 1946; Howard and Childs, 1959), *T. monticola* (Ingles, 1952), and *G. bursarius* (Wilks, 1963) have been reported to have distinct breeding seasons with little reproduction at other times. Williams and Baker (1976) have reported that *P. castanops* is reproductively active throughout most of the year with the possible exception of October and November. This longer season would allow adult *Pappogeomys* to produce as many as three litters per year.

The mean litter size of 2.0 reported for *Pappogeomys* by Ickenberry (1964) is low when compared to 4.6 (Howard and Childs, 1959) and 5.7 (Miller, 1946) reported for *T. bottae*. *Thomomys* populations are characterized by a sharply defined peak period of recruitment and increased density. Populations of *Pappogeomys*, on the other hand, maintain relatively constant low levels of recruitment. This continuous low reproductive output through a longer breeding season produces a population with a complex age structure, and may provide a buffer to randomly directed environmental catastrophes, such as flooding (Williams and Baker, 1976), fires, or, most important to arid-land inhabiting animals, seasonal droughts. A catastrophe that either drastically reduces or inhibits reproduction in the core of adults of a population with a highly synchronized breeding season, could disrupt the age structure to the extent of causing a population crash or even extinction. This is especially possible for populations of *Thomomys* and *Geomys*, which produce all their new recruits, especially males, in a narrow peak season. The existence of a well-developed subadult age class, especially young males (on the average, males in our samples live only two-thirds as long as females), can offer insurance against such short-termed seasonal catastrophes in *Pappogeomys*.

An additional advantage of the reproductive strategy of *P. castanops* may exist in the form of more random male-female matings. *Thomomys* and *Geomys*, which have few, but large litters per year, may produce many offspring that are the product of but one male. This would encourage a rapid shift in genetic composition of the population toward that of reproducing males. A longer reproductive season with small litters could allow more males to participate in reproduction, even young of the year, thereby moderating the potential effects of genetic drift.

Small population size and inbreeding can easily reduce genetically controlled variability. The chance of inbreeding among individuals within the population is affected by the movement patterns and home range arrangements among the sexes and age classes. The home range of gophers is synonymous with their territory in that the daily movements are restricted to the defended burrow system. The home ranges of *Pappogeomys* are relatively stable, as they are with *Thomomys bottae* (Ingles, 1952; Howard and Childs, 1959). Modifications of the home range size were observed, and

were probably due to minor shifts caused by density or lack of local resources. Adult females had the most stable home range size, whereas males were more prone to movement. Female *Pappogeomys* were distributed so that the density of the individuals, especially of the adult females, was low. The result was a patchy distribution of females. Male *Pappogeomys*, on the other hand, arrange their home ranges so as to contact the home ranges of more animals, especially females. This was apparent at the beginning of intense reproduction in January, when the density of gophers was 4.3 animals per male home range.

This type of distribution may be related to recruitment patterns. Spacing in adult females leaves intermediate areas available for colonization by offspring. This phenomenon was observed in the relationship of adult female F-11 with her progeny (Fig. 6). Three of her five offspring (one male, two females) colonized the area immediately adjacent to her home range, whereas the other two (one male, one female) moved longer distances to the vacant areas near two other females. Colonization of the area near the maternal home range provides a degree of insurance that gophers will inhabit the area in the future, whereas those moving longer distances provide the genetic mixing which would reduce the amount of inbreeding within the population. If adult females were compacted into adjoining home ranges, all their offspring would be required to move longer distances to colonize, and thus be subjected to higher mortality levels (Howard and Childs, 1959).

In some aspects, members of the genus *Pappogeomys* are less variable than those of the genera *Thomomys* and *Geomys*. An example of these differences is seen in the published chromosomal data. Six species of *Pappogeomys* have been karyotyped and five different karyotypes are known (Berry and Baker, 1972; Laguarda-Figueras et al., 1971; Hart and Patterson, 1976). In the genus *Geomys*, five species have been karyotyped and over 25 karyotypes have been described (Davis et al., 1971; Baker et al., 1973; Selander et al., 1974; Hart, 1978; Williams and Genoways, 1975). It is unclear exactly how many cytotypes represent distinct species of *Thomomys*, but at least nine species, revealing over 30 karyotypes have been described (Patton, 1973; Patton and Dingman, 1968, 1970; Thaeler, 1968, 1972, 1973; Wentworth and Sutton, 1969; Berry and Baker, 1971). Thus, both *Thomomys* and *Geomys* have five times as many described chromosomal types as does *Pappogeomys*. It is our hypothesis that the sample of karyotypes generally reflects the overall patterns of chromosomal variation in the three genera.

Wilson et al. (1975) and Bush et al. (1977) have proposed that breeding structure and deme size are the most critical factors promoting chromosomal evolution. Are there differences in the population and breeding structure among the species of these three genera that can account for part or all of the observed differences in chromosomal variation? Our estimates of the population parameters of *Pappogeomys castanops* indicate that the effective breeding population in this species is as low or lower than the values reported for *Thomomys* and *Geomys*; therefore, population size alone does not distinguish *Pappogeomys* from *Geomys* and *Thomomys*. There is one major aspect, however, of the reproductive biology of *Pappogeomys* that may account for some of the differences. *Pappogeomys* has smaller and more litters per year, and a longer breeding season than both *Thomomys* and *Geomys*. Such a reproductive strategy would result in fewer population fluctuations and a greater probability of more crosses between different individuals. These breeding differences could be important in maintaining a more stable population in *Pappogeomys* which might not be as likely to go through bottlenecks, which would produce drift. The breeding strategies of *Thomomys* and *Geomys*, on the other hand, would appear more likely to promote population fluctuations in numbers of breeding individuals required to produce genetic drift. If this observation has meaning, then the greater amount of variation in *Thomomys* and *Geomys* is primarily a product of genetic drift due to population fluctuations.

There are other alternative explanations which are worthy of consideration. Chromosomal variation with altered regulator genes has been proposed as a means of producing morphological change (Wilson et al., 1974) and it is possible that the larger amounts of morphological variation in *Thomomys* and *Geomys* are partially the result of chromosomal evolution. In addition, studies on a population of *Geomys* (Patton et al., in press) reveal that in this specific case, a chromosomal heterozygote has an adequate selective advantage to be maintained in the face of (1) any meiotic problems resulting from being heterozygous for a centric fusion between unequal-sized acrocentrics, and (2) inbreeding as a result of low vagility and low population size. If the conclusion of Patton et al. (in press) that the heterozygote meiotic bottleneck may not always be a deterrent to chromosomal evolution that prior discussions have suggested is true, then the need for low deme size and drift may not be as important in the evolution of chromosomes as recent papers have suggested (Bush et al., 1977; Lande, 1979).

The primary differences observed between life history strategies of *Pappogeomys castanops* as compared with other geomyids are those concerning reproductive parameters. However, it is not known whether this difference is in fact due to a genetic adaptation or rather to a physiological response to differences in caloric food values and/or the presence of a stimulant to reproduction in the vegetation, as described to affect microtines (Berger and Negus, 1974). This difference in reproduction, coupled with intense mixing of breeding pairs throughout the reproductive life of the females and high vagility would be sufficient to reduce genetic variability within and among populations, subspecies, and species. These are hypotheses which must now be tested.

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