

# Vagility and Local Movements of Pocket Gophers (Geomyidae: Rodentia)

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**ABSTRACT:** A 2-year live-trap study in the Davis Mountains of Texas was conducted in a zone of sympatry between *Pappogeomys castanops* and *Thomomys bottae*.

*Thomomys bottae* demonstrated low levels of vagility. *Pappogeomys castanops* demonstrated high levels, particularly in adult males and sub-adult females. Individual movements of *P. castanops* showed a significant directional trend toward the population of *T. bottae*. Individual movements of *T. bottae* showed no distinct directional trends.

*Thomomys bottae* is generally restricted to areas of high soil moisture, while *Pappogeomys castanops* is not restricted by this factor. In addition, the population size and structure of *P. castanops* and flood erosion of *T. bottae* habitat may further contribute to the replacement of *T. bottae* by *P. castanops*. Although other factors may allow the replacement of these pocket gophers, major displacement may be the result of severe environmental conditions in the form of intense flooding or aridity.

## INTRODUCTION

Vagility, the potential or ability to disperse, is an important characteristic influencing many biological aspects of a species, such as the rate and degree of population growth, gene flow and morphological divergence. Vagility, in turn, may be affected by gross morphology, behavior, physiology, natural history and population dynamics of the species (Udvardy, 1969). Organisms with limited vagility encounter problems involving range expansion, maintenance of heterozygosity and complete dependence on local environment.

Pocket gophers (Geomyidae) have low vagility (Patton *et al.*, 1972). These animals are adapted to a herbivorous fossorial habit (Patton, 1972), which obviously restricts the vagility of a species. The morphological adaptations of pocket gophers cause them to be awkward and vulnerable outside their burrows.

In the location selected for this study, *Thomomys bottae limpiae* and *Pappogeomys castanops pratensis* occur sympatrically (Reichman and Baker, 1972). This locality was favorable because the habitat was relatively undisturbed, the areas occupied by pocket gophers were restricted, both genera could be studied simultaneously under similar environmental conditions, and possible movements were detected in previous studies (Reichman and Baker, 1972). Because geomyid rodents are not known to have subdivided the fossorial habitus (Russell, 1968), vagility may be particularly important to pocket gophers when different species are sympatric.

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## METHODS AND MATERIALS

This study was conducted 9.0 km N, 9.5 km E of Fort Davis, Jeff Davis Co., Texas, between May 1971 and August 1973. Intensive live-trapping (Baker and Williams, 1972) was conducted in an area which extended 250 m on either end of the zone of sympatry. Trapping was occasionally extended to other areas to determine the local distribution of both species. Trapping was conducted twice a month in 1971 except for once a month in August and December. During 1972 and through February 1973, trapping was conducted once a month, except in June, August and December when no trapping was performed.

An aerial photograph (dated 16 March 1971; obtained from the Department of Interior, Geological Survey) was used to map the zone of sympatry, plot individual capture sites, and determine distance and direction of movements. This method of recording localities proved to be reasonably accurate ( $\pm 5$  m) and easily used, even in large areas with irregular terrain.

Each pocket gopher captured was coded according to species (P = *Pappogeomys*; T = *Thomomys*), sex ( $\sigma$ ;  $\phi$ ), sequential collecting number and age (A = adult; S = subadult, juvenile). Specimens were toe-clipped and released at the capture site. The suggestions of Howard and Ingles (1951) concerning methods of studying fossorial mammals were incorporated. Excavation of burrow systems was restricted to preserve the habitat. The extent and complexity of burrow systems were indicated by multiple trappings of individual pocket gophers. Sex was verified by checking the pubic symphysis, mammae or baculum. Age determination in both species was primarily based on pelage (Bailey, 1915; Morejohn and Howard, 1956) as juvenile, subadult or adult.

The home range of pocket gophers is restricted to the burrow system (Turner *et al.*, 1973; Wilks, 1963). Because this study is primarily concerned with dispersal tendencies beyond the burrow system, the actual area of the home range as treated by other investigators (Howard and Childs, 1959; Turner *et al.*, 1973; Wilks, 1963) is not critical. However, the size of the burrow system, or home range at any specific time, is important in differentiating movements within a single burrow system and movements into new areas. Our technique involved deriving a conservative estimate of the extent of the burrow system and eliminating all movements that were less than this estimate. Because small movements could not be properly evaluated and the dispersal capabilities were of primary interest, this study was mostly concerned with larger movements.

Estimates of the extent of burrow systems were obtained by determining the maximum distance between capture sites of any individual in 24 hr, because it is unlikely that a pocket gopher will move into a new area, establish its territory, and build a new burrow system within such a short period of time. Therefore, distances less than the length of a burrow system, as determined above, were considered as movements within a single burrow system, whereas greater distances

were treated as movements into new areas.

Because pocket gopher habitat in Limpia Canyon is a narrow zone paralleling the creek, nearly all movements could be recorded as either upstream or downstream from previous capture sites. A chi-square goodness of fit test (Sokal and Rohlf, 1969) was used to determine if direction of movements, either upstream or downstream, was random. If multiple movements of an individual showed opposing directions, the directional trend was determined as the difference between distances traveled upstream and downstream.

Statistical analyses of individual movements were conducted using Power's UNIVAR program (Power, 1970). Individual movements were grouped according to age, sex and species. Comparisons were made using average distance of all movements, total distance of movements exceeding the prescribed burrow length, and total distance of all movements. The average distance indicates the possible size of the home range (Davis, 1953), whereas the total distance of movements exceeding the burrow length was taken as indicative of actual dispersal tendencies. The total distance combines the movements in and out of the burrow system and provides a general evaluation of vagility.

Assuming the burrow system to equal the size of the home range, it was possible to estimate the geographical limits of the population by establishing a standard home range for individual pocket gophers, based on estimated burrow lengths of each species. Using this method for each capture site, estimates of the habitat and distribution of both species were made and compared. These estimates indicate the general distribution trends for the duration of the study. Population movements were determined by noting geographic location and numbers of captured individuals along the population margins.

Monthly precipitation records from 1931 to 1973 for the weather station at Fort Davis, Texas, were obtained from the statistical reports of the United States Weather Bureau (U.S. Department of Commerce, 1931-1973) and were examined to determine if rainfall could be correlated with geographical changes of distribution as suggested in the literature (Blair, 1939, 1940; Davis and Beuchner, 1946; Reichman and Baker, 1972).

A monthly determination of soil moisture provided a means of testing selection of soil types by *Thomomys bottae* and *Pappogeomys castanops*. Soil samples were collected from June 1971 to May 1972 at three depths (15, 30 and 45 cm) in 10 localities throughout the trapping area. To reduce sampling error, five samples were taken at each depth at each locality. The localities were selected according to capture sites of five *P. castanops* and five *T. bottae* and were assumed to represent suitable habitat. Moisture content was determined by gravimetric analysis. Samples were compared using Power's UNIVAR program (Power, 1970).

Records of frequency and magnitude of floods were recorded by a flood stage meter located in the study area and were obtained from the Water Resources Division of the United States Department of Interior,

Geological Survey in San Angelo, Texas.

### RESULTS

During this study, 77 *Pappogeomys castanops* and 122 *Thomomys bottae* were marked in the zone of sympatry. Of these, 81 were recaptured up to six times, resulting in 317 captures. At least 65 other pocket gophers were collected outside the study area.

Movement data of the pocket gophers, grouped according to age, sex and species, are presented in Table 1. The  $F_s$  value and level of significance between groups are presented in Table 2. Data for subadult

TABLE 1.—Sample sizes (N), means ( $\bar{X}$ ) ranges, and standard errors (S.E.) of movement data of pocket gophers grouped according to age (A=adult; S=subadult), sex ( $\delta$ ;  $\phi$ ), and species (P=*Pappogeomys*; T=*Thomomys*). Means and ranges are given in meters

		A $\delta$ P	A $\phi$ P	S $\phi$ P	A $\delta$ T	A $\phi$ T	S $\delta$ T	S $\phi$ T
AVERAGE DISTANCE	N	8	13	7	11	29	4	9
	$\bar{X}$	217.81	46.22	435.71	31.83	28.36	8.32	20.56
	Range	5-495	5-100	5-270	10-81.7	0-120	0-20	0-50
	S.E.	$\pm 69.22$	$\pm 8.91$	$\pm 136.68$	$\pm 8.44$	$\pm 5.29$	$\pm 4.25$	$\pm 4.44$
TOTAL DISTANCE OF MOVEMENTS EXCEEDING THE BURROW LENGTH	N	5	6	5	4	9	0	0
	$\bar{X}$	391.00	85.00	185.00	112.50	74.44	0.00	0.00
	Range	135-595	60-100	65-340	55-215	45-120	0	0
	S.E.	$\pm 82.88$	$\pm 7.30$	$\pm 52.58$	$\pm 36.08$	$\pm 7.97$	$\pm 0.00$	$\pm 0.00$
TOTAL DISTANCE	N	8	13	7	11	29	4	9
	$\bar{X}$	256.88	60.38	137.14	66.36	44.14	8.32	20.56
	Range	5-625	5-130	5-350	0-245	0-150	0-20	0-50
	S.E.	$\pm 85.87$	$\pm 10.35$	$\pm 49.30$	$\pm 21.32$	$\pm 7.39$	$\pm 4.25$	$\pm 4.44$

male *Pappogeomys* and total distance of the prescribed burrow length for subadult *Thomomys* were omitted because of insufficient data. Individual movements are plotted on a map of the study area (Fig. 1). The greatest distance measured for *P. castanops* in 24 hr was 50 m, whereas the greatest distance for *T. bottae* was 40 m. These measurements were used as the burrow length for each species. Records of time required to make longer movements were more difficult to ascertain.

TABLE 2.—Levels of significance (subscript) and  $F_s$  values derived from comparisons of movements grouped according to age (A=adult; S=subadult), sex ( $\delta$ ;  $\text{♀}$ ), and species (P=*Pappogeomys*; T=*Thomomys*). Coding used in this table is as follows: 0=0.0; 1=0.25; 2=0.50; 3=0.75; 4=0.90; 5=0.95; 6=0.975; 7=0.99; 8=0.995; 9=0.999; "X"=unknown values due to insufficient data

		A $\delta$ P	A $\text{♀}$ P	S $\text{♀}$ P	A $\delta$ T	A $\text{♀}$ T	S $\delta$ T	S $\text{♀}$ T
AVERAGE DISTANCE	A $\delta$ P							
	A $\text{♀}$ P	9.87 <sub>7</sub>						
	S $\text{♀}$ P	2.19 <sub>4</sub>	15.59 <sub>9</sub>					
	A $\delta$ T	9.86 <sub>7</sub>	1.34 <sub>1</sub>	14.09 <sub>8</sub>				
	A $\text{♀}$ T	27.06 <sub>9</sub>	3.26 <sub>4</sub>	39.40 <sub>9</sub>	0.12 <sub>1</sub>			
	S $\delta$ T	4.36 <sub>4</sub>	5.22 <sub>5</sub>	5.33 <sub>5</sub>	2.62 <sub>3</sub>	1.90 <sub>3</sub>		
	S $\text{♀}$ T	9.16 <sub>7</sub>	5.07 <sub>5</sub>	12.09 <sub>8</sub>	1.22 <sub>2</sub>	0.62 <sub>2</sub>	2.78 <sub>3</sub>	
TOTAL DISTANCE OF MOVEMENTS EXCEEDING THE BURROW LENGTH	A $\delta$ P							
	A $\text{♀}$ P	16.54 <sub>8</sub>						
	S $\text{♀}$ P	4.40 <sub>4</sub>	4.31 <sub>4</sub>					
	A $\delta$ T	7.89 <sub>5</sub>	0.84 <sub>2</sub>	1.15 <sub>2</sub>				
	A $\text{♀}$ T	27.23 <sub>9</sub>	0.84 <sub>2</sub>	7.87 <sub>6</sub>	2.18 <sub>3</sub>			
	S $\delta$ T	X	X	X	X	X		
	S $\text{♀}$ T	X	X	X	X	X	X	
TOTAL DISTANCE	A $\delta$ P							
	A $\text{♀}$ P	8.46 <sub>7</sub>						
	S $\text{♀}$ P	1.35 <sub>2</sub>	4.06 <sub>4</sub>					
	A $\delta$ T	6.17 <sub>6</sub>	0.07 <sub>1</sub>	2.25 <sub>3</sub>				
	A $\text{♀}$ T	21.72 <sub>9</sub>	1.55 <sub>3</sub>	11.33 <sub>8</sub>	1.59 <sub>3</sub>			
	S $\delta$ T	3.99 <sub>4</sub>	7.34 <sub>6</sub>	3.72 <sub>4</sub>	2.56 <sub>3</sub>	3.14 <sub>4</sub>		
	S $\text{♀}$ T	8.56 <sub>6</sub>	9.30 <sub>7</sub>	7.24 <sub>6</sub>	3.64 <sub>4</sub>	3.01 <sub>4</sub>	2.78 <sub>2</sub>	

Although such movements probably require a short time, data indicated individuals of *P. castanops* making movements of 270 m in 20 days, 65 m in 8 days, and 100 m in 21 days. Individuals of *T. bottae* moved 95 m in 75 days, 65 m in 29 days, 45 m in 82 days, and 80 m in 84 days.

*Pappogeomys castanops* makes longer movements than *Thomomys bottae* (Fig. 1). Adult male *Pappogeomys* made the longest total movements (maximum 625 m), followed by subadult female *Pappogeomys* and adult female *Pappogeomys*. The greatest total distance moved by *T. bottae* was also by adult males (maximum 245 m). The order of length of movements following the adult male *Thomomys* was adult female *Thomomys*, subadult female *Thomomys* and subadult male *Thomomys*. Some individuals of *Thomomys* did not move during a period of several months (Tables 1 and 2).

In many areas, movements of pocket gophers allowed replacement of individuals of the same species and reutilization of burrow systems. This replacement was first noticed when a *Pappogeomys* was killed in a trap. One week later this burrow was occupied by another *Pappogeomys* which had previously been captured 270 m away. Eight months later another *Pappogeomys* moved 45 m to the same site. There were at least three other cases of conspecific replacement in *Pappogeomys*. At one site a *Thomomys* was trapped in July 1971, and a month later another *Thomomys* was collected at the same site. It was later discovered that the original occupant had moved 85 m upstream. However, by this time the collecting site of both individuals was occupied by

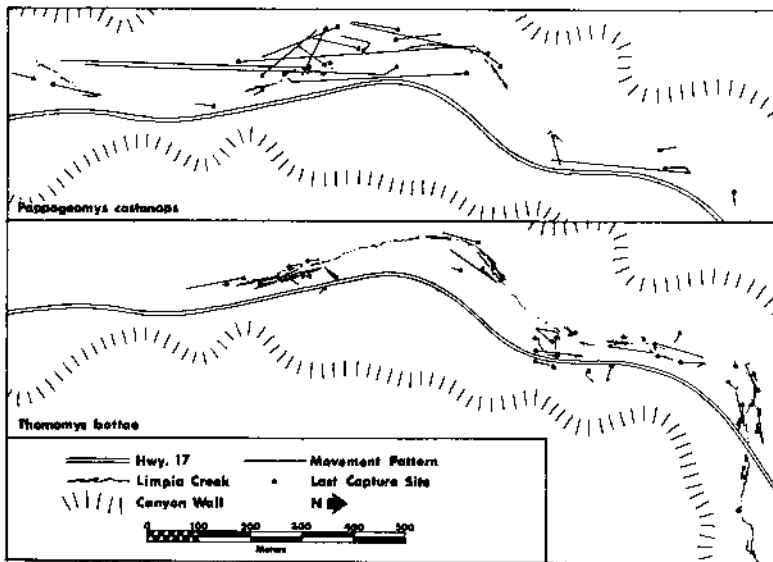


Fig. 1.—Individual movements of *Pappogeomys castanops* and *Thomomys bottae* in the study area. Note differences in distance traveled by both species and the isolated groups of *T. bottae*

a third *Thomomys*. At least three other conspecific replacements occurred between individuals of *Thomomys*. Some trap sites produced both species at different times during the study, but there was no evidence to suggest that either utilized the burrow system of the other.

A majority of the *Thomomys* ( $N = 46$ ,  $\chi^2 = 0.82$ ) moved downstream, but the difference in direction was not significant. Individuals of *Pappogeomys* ( $N = 25$ ,  $\chi^2 = 4.84$ ) showed a significant ( $P \geq .95$ ) directional trend downstream.

Throughout the zone of sympatry some regions were never occupied by either species, while other areas were inhabited by one or both species. In some instances groups of individual pocket gophers were isolated from the main population (Fig. 2). Fluctuations in population boundaries were noted but revealed no unusual directional trend in either population. Although on rare occasions individual pocket gophers suggested that boundary shifts had occurred, such instances were explained to result from dispersal, death or escape from previous trapping efforts.

During the 2 years of this study, *Thomomys bottae* inhabited 72.6% of the suitable fossorial habitat in the zone of sympatry, whereas *Pappogeomys castanops* occupied 59.6%. The difference between these values indicates that the actual zone of sympatry between the two species is only 13.0% of the suitable habitat.

The population size of *Thomomys bottae* remained relatively stable. Sex ratios always favored females with ratios of 2.4:1 in 1971, 3.4:1 in 1972, and 2.8:1 in 1973. *Pappogeomys* showed a drop in population density. Sex ratios in this species also favored females with ratios of 1.8:1 in 1971, 2.6:1 in 1972, and 2.7:1 in 1973. The ratio of individuals of *T. bottae* to individuals of *P. castanops* increased as the population size of *P. castanops* dropped. In 1971 and 1972 the ratio of *Thomomys* to *Pappogeomys* was 1.2:1, and increased to 3.0:1 in 1973.

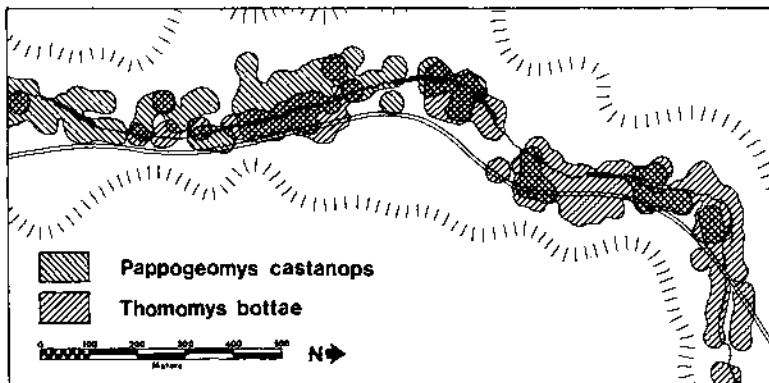


Fig. 2.—Distribution, determined from individual capture sites (see text), of *Pappogeomys castanops* and *Thomomys bottae* in the study area. Note the discontinuity of populations of both species

Low precipitation (27.99 mm; mean annual precipitation obtained from available records since 1931 is 38.4 cm) during 1971 resulted in one of the driest years since the middle 1950's. There was no substantial precipitation until July. Most rains came in August and progressively decreased until the end of the year. Precipitation during 1972 was 47.40 cm, with the heaviest rains occurring in May, August and September.

Monthly means of soil moisture at all depths were usually higher in areas inhabited by *Thomomys bottae* than in areas inhabited by *Pappogeomys castanops* (Fig. 3). The degree of difference between representative sites decreased as depth increased. At 15 cm, high levels of difference were found during every month except September ( $P \geq .90$ ). At 30 cm, significant differences in soil moisture were noted in all months except October, December, January and May ( $P \geq .90$ ). At 45 cm, only samples taken in June, November and February were significantly different ( $P \geq .90$ ). The mean burrow depth (*Thomomys* = 18.6 cm; *Pappogeomys* = 25.7 cm) of each species fell between the first two depths where samples were taken.

#### DISCUSSION

The study area was representative of the Chihuahuan Desert and was restricted on two sides by steep canyon walls. Such a situation may be relatively unusual among areas of sympatry between pocket gophers.

The vagility of *Pappogeomys castanops* was indicated by its ability to travel long distances in a short time. Because of the large distances

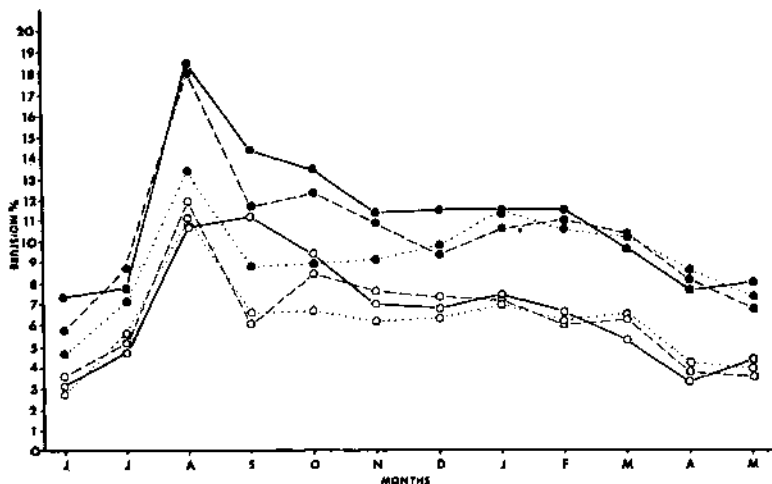


Fig. 3.—Graphical representation of changes in mean soil moisture between June 1971 and May 1972. The solid dots and open dots represent soil moisture at *Thomomys* and *Pappogeomys* localities, respectively. The solid line, broken line and dotted line indicate soil moisture at depths of 15, 30 and 45 cm, respectively

between capture sites and the irregular terrain of the study area, it is assumed that *P. castanops* moves overland. This study showed adult males and subadult females have the greatest dispersal tendencies of all groups studied. It is suspected that movement patterns of subadult males, which are presently unknown, will be comparable to movements of adult males and subadult females. In addition to extensive movements adult male and subadult female *Pappogeomys* have large home ranges.

The cause for directional movements in *Pappogeomys* is not known. This trend may result from population pressure further up the canyon. Noncompatible intraspecific behavior in *Pappogeomys* may cause individuals to be more successful in moving into areas occupied by *Thomomys* than into conspecific areas. Because *Thomomys* is more successful in moving into areas occupied by other *Thomomys*, it is suggested that *Pappogeomys* may be more aggressive than *Thomomys*.

This study suggests that vagility in *Thomomys bottae* is relatively low as compared to that of *Pappogeomys castanops*. There was a remarkable similarity in the limited dispersal tendencies among different age and sex groups. It might be expected that one sex would show greater vagility as a result of difference in sexual behavior, but this was not the case. Also, it would seem likely that subadults would show greater vagility than adults if they are to find suitable habitat for themselves. However, subadults had shorter movements than adults.

The burrow length of 40 m for *Thomomys* approximates the described length of the home range (Howard and Childs, 1959; Ingles, 1952; Turner *et al.*, 1973). Howard and Childs (1959) suggested most movements outside the home range, by *T. bottae* in California, do not represent movements into entirely new areas but, instead, represent boundary shifts by employing reutilization and abandonment of portions of burrow systems. Movements up to 120 m were noted. Vaughan (1963) reported mean maximum movements of 135 m in *T. bottae* introduced into new areas. In Limpia Canyon, dispersal patterns of *T. bottae* were comparable to the studies of Howard and Childs (1959) and Vaughan (1963). The greatest single distance was 130 m. Because extensive movements required considerable time, burrowing activities may represent the primary means of dispersal for *T. bottae* in Limpia Canyon.

If *Thomomys bottae* does not actually make movements into entirely new areas, then the isolating tendencies are more readily explained. Not only were groups isolated from each other and the main population (Fig. 2), but also there was no exchange of individuals between these groups (Fig. 1). Apparently these isolating tendencies are common in *Thomomys* populations (Patton and Dingman, 1968; Thaeler, 1968; Vaughan, 1967). With such tendencies so apparent on a small scale it is conceivable how a lack of gene flow would eventually result in a high degree of subspeciation as seen in the genus *Thomomys* (Hall and Kelson, 1959).

Because individuals of *Thomomys bottae* replace each other and the

local distribution of this species is occasionally discontinuous and confined to areas around Limpia Creek (Williams, 1976), it is suggested that individuals are often restricted by the limits of the available and suitable habitat. Habitat selection in pocket gophers is well-documented. Ingles (1949) noted seasonal changes in pocket gopher distribution due to groundwater and snow. The distribution of species and local populations has been explained on the basis of soil types (Best, 1973; Davis *et al.*, 1938; Davis, 1940). Judd and Reichman (1972) suggested the necessity of succulent vegetation for some geomyid rodents. In Limpia Canyon, soil moisture was a critical factor for *T. bottae*. Because soil moisture is affected by several variables such as precipitation, temperature, runoff, vegetation and soil type, consistent records of high moisture levels stress the possible importance of this factor to *Thomomys*. It is not certain whether *Thomomys* was selecting soil with high moisture or selecting associated vegetation or soil types. It is assumed that soil moisture may be the most important factor because similar vegetation and soil types occurred in areas not inhabited by *Thomomys*.

The success of *Pappogeomys castanops* in replacing *Thomomys bottae* appears to be due to its broader habitat requirements and greater vagility. Previously, little was known about these characters in *P. castanops*. Judd and Reichman (1972) pointed out that *P. castanops* is capable of successfully using less succulent foods than *T. bottae*. Reichman and Baker (1972) noted *P. castanops* occurred in a wide range of habitats, ranging from the mesic habitat of *T. bottae* to more xeric habitats away from the creek. The local distributions of *P. castanops* outside the study area and soil analyses of characteristic habitats further suggest the ubiquitous nature of this species.

The attributes of *Pappogeomys castanops* would probably allow replacement of *Thomomys bottae* by direct competition with sufficient time. Range extension is probably achieved when *P. castanops* invades areas left unoccupied by *T. bottae* (Reichman and Baker, 1972). Because the distribution of both species has been relatively stable, other factors must be promoting the replacement of *Thomomys*. Reichman and Baker (1972) discussed how differential reproduction and the association of floods and drier climates might contribute to this trend. Another possible mechanism occurs when burrow systems on the banks of Limpia Creek are exposed by flood erosion. Because *T. bottae* generally has shallower burrow systems, it is probably affected more by the floods than *P. castanops*. Even though most individuals survive the floods, *T. bottae* is not apt to reclaim eroded areas (Williams, 1976); thus subsequent occupation of *P. castanops* is possible. Such erosion is characteristic of years without spring rains to establish vegetation to curtail the force of the floods (Williams, 1976).

Another important factor in the success of *Pappogeomys castanops* replacing *Thomomys bottae* is the population size and structure at times when the opportunity to claim more territory exists. Because most movements of *P. castanops* are made by adult males and subadult fe-

males, success of colonization not only depends on the population size but also the number of individuals included in these groups. Colonization by *P. castanops* would probably be most successful when a large population with a high ratio of adult males and subadult females exists. Such a combination of factors would provide expansion pressure and a means for colonization. The degree of success would probably vary according to the total amount of dispersal pressure in the *Pappogeomys* population working against the total amount of dispersal pressure in the *Thomomys* population. Because *T. bottae* does not demonstrate high vagility as a species, or individually by age or sex, its population size and structure are not important when considering its impact on *P. castanops*.

Although the suggested mechanisms may have a definite effect on the ability of *Pappogeomys castanops* to replace *Thomomys bottae*, their impact on past displacement is questionable. It appears that there was some degree of sympatry between both species as early as 1937. At this time, *P. castanops* was collected 1.6 km N of Fort Davis (Blair, 1940), and *T. bottae* was reported from 1.6 km N of Fort Davis (Blair, 1939), 1.6 km NW of Fort Davis and 3.2 km NW of Fort Davis (Blair, 1940). Blair (1940) pointed out the "stream-bed association" of *T. bottae* and "short grass association" of *P. castanops* which still persists today. Data taken from study specimens at the Texas Wildlife Research Collection (Texas A&M University, College Station, Texas) suggest the geographical distribution of both species was unchanged at least until 1941. Davis and Beuchner (1946) reported collecting topotypes of *T. bottae* and indicated, from distributional descriptions of *P. castanops*, that both species were still sympatric. However, in 1968, the geographical distribution of *T. b. limpiae* was reported to have receded 13 km to 9.0 km N, 9.5 km E of Fort Davis. In spite of this change, *T. bottae* and *P. castanops* are still sympatric and maintain the same ecological associations (Reichman and Baker, 1972). The present study has indicated no major changes in the geographical distribution or ecological associations of either species. To explain the present location of *T. bottae* in Limpia Canyon, it would be necessary for this population to recede over 400 m each year. Because this has not been the case between 1937 and 1941, and 1968 and 1973, it is doubtful that the described mechanisms have played a major role in past displacement.

The population of *Thomomys bottae* has probably been sporadically distributed along Limpia Creek in the past. Great distances between colonies would facilitate greater recession rates if isolated populations die out. The occurrence of such colonies is supported by the isolated groups of pocket gophers in the study area.

Assuming that isolated colonies once existed, the cause for their disappearance is still not explained. It is suggested that the current distribution of *Thomomys* in Limpia Canyon has probably been the result of one or more periods of severe environmental conditions. Several events have occurred since 1941 that may have contributed to

the present conditions. Although there were no significant fluctuations in population boundaries in 1971, xeric conditions may become more critical if the condition persists. This may have been the case during the drought of the early 1950's. Annual precipitation was exceptionally low for six consecutive years. During this time it is possible that populations of *T. bottae* were greatly reduced from the prolonged lack of suitable vegetation and habitat. Similarly, it is feasible that abnormal flooding could easily eliminate individual pocket gophers and possibly small isolated populations. In 1946 and 1966 there was extensive flooding in Limpia Canyon (Williams, 1976).

There may be other factors which make it possible for *Pappogeomys* to replace *Thomomys*. Undoubtedly, replacement may be affected by other factors or combination of factors in areas where *Pappogeomys* occurs with, or has replaced, other pocket gopher populations (Baker *et al.*, 1973; Hall and Villa-R, 1949; Russell, 1968; Williams and Baker, 1974). However, the area of sympatry between *P. castanops* and *T. bottae* in Limpia Canyon is still of considerable interest, and if further analysis of this problem is continued, care should be taken so that the future of these pocket gophers is not influenced or jeopardized.

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