ECOLOGICAL SEPARATION OF THREE GENERA OF POCKET GOPHERS (GEOMYIDAE)

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ECOLOGICAL SEPARATION OF THREE GENERA OF POCKET GOPHERS (GEOMYIDAE)[1]

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Abstract. A study of the ecology and distribution of *Geomys bursarius jugossicularis* Hooper, *Thomomys bottae cultellus* Kelson, and *Pappogeomys castanops* Baird was conducted in northeastern New Mexico. Comparisons of body size, soils utilized, burrow characteristics, distinguishing surface features, and winter activity revealed each species to be ecologically separate. Altitude and soils are discussed as factors influencing the geographical separation of the species, although soil appears to be the primary limiting factor. Based on the observed distribution and range of soils inhabited, the most limited distribution and the broadest range of soil types is found for the largest species *P. castanops*, followed by *T. bottae* and then *G. bursarius*.

Introduction

Pocket gophers of the family Geomyidae form a genetically plastic, morphologically similar group of five extant genera: *Thomomys*, *Zygogeomys*, *Geomys*, *Orthogeomys*, and *Pappogeomys* [= *Cratogeomys*] (Russell 1968*a*). The group ranges from southern Canada to Panama, becoming transcontinental in distribution from the southern United States through Central America. The ranges of pocket gophers generally do not overlap (Bailey 1926, Grinnell 1926, Storer 1933, Goldman 1939, Quimby 1942, Baker 1956, Youngman 1958, Patton and Dingman 1968), and even in areas where two species are found in close proximity they are probably ecologically separated. *Pappogeomys* and *Thomomys* exist together in portions of Mexico and southwestern Texas (Davis 1940*b*, 1944, Davis and Robertson 1944, Hall and Villa-R 1949, Blair and Miller 1949, Baker 1953, Reichman and Baker 1972). In these areas *Thomomys* is usually restricted to the hard or shallow soils, whereas *Pappogeomys* usually occurs in the deeper sandier soils; their occurrence in the same area seems to be the exception rather than the rule. Where *Geomys* and *Thomomys* occur in the same vicinity, the former is usually found in the deeper soils and *Thomomys* on higher ground in firmer soil (Jones 1964). The same is true when *Geomys* and *Pappogeomys* meet, i.e., *Geomys* in deep soils and *Pappogeomys* in elevated, firm soil (Cary 1911, R. S. Miller 1964).

The ranges of *Geomys, Pappogeomys*, and *Thomomys* approach each other in southeastern Colorado and northeastern New Mexico (Hall and Kelson 1959). Cary (1911), Hansen et al. (1960), and R. S. Miller (1964) have studied the distribution of the three genera in Colorado and found them to be allopatric. Pocket gophers have not been studied previously in northeastern New Mexico, where during the present investigation I evaluated the ecological requirements and the local factors affecting the distributions of *T. bottae cultellus* Kelson, *G. bursarius jugossicularis* Hooper, and *P. castanops* Baird.

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Methods

Union County, New Mexico, was selected for study following a preliminary survey in 1966 which revealed *Geomys*, *Pappogeomys*, and *Thomomys* occurring in close proximity. I collected 127 pocket gophers from 83 localities within the county. Most specimens were collected from May to early July 1968 with Victor and Macabee kill traps. Specific localities and elevations were determined with U. S. Geological Survey maps (nos. NJ 13-12 and NI 13-6, Scale, 1: 250,000); all specimens were prepared as standard study skins and skulls and were deposited in the Eastern New Mexico University Natural History Collection and the collection of recent mammals at the University of Oklahoma Stovall Museum of Science and History.

At the point where the burrow system was opened I sketched the approximate shape of its cross-section, measured the greatest diameter and depth below the surface, and noted the general vegetation and topography of the collection site. The size, shape, and number of mounds, as well as signs of surface activity by gophers and their ecological associates were also recorded.

Surface soil texture, subsoil texture, permeability, slope, and depth of soil were determined for each collecting locality from maps made available by personnel of the U. S. Department of Agriculture, Soil Conservation Service, in Clayton, New Mexico. Soil textures (surface and subsoil) were given as clay, clay-loam, loam, sandy-loam, and sand. The Soil Conservation Service has assigned values of 1 to 5, respectively, to the groups. Soil permeability was

TABLE 1. Comparison of external body measurements (mm) and weights (g) of adult Geomyidae[a]

	SPECIES			COMPARISONS		
	(1) *Geomys bursarius*	(2) *Pappogeomys castanops*	(3) *Thomomys bottae*	1 vs. 2	1 vs. 3	2 vs. 3
Total length	♂ 263.5 (15;12.258)	♂ 289.3 (13;10.973)	♂ 231.0 (13; 9.028)	*	*	*
	♀ 246.7 (15; 8.489)	♀ 266.9 (13;10.420)	♀ 216.2 (17; 6.267)	*	*	*
Length of tail vertebrae	♂ 80.3 (15; 4.399)	♂ 83.9 (13; 7.632)	♂ 70.5 (13; 6.398)		*	*
	♀ 75.3 (15; 4.334)	♀ 74.2 (13; 5.847)	♀ 65.6 (17; 5.455)		*	*
Body length	♂ 183.3 (15;10.032)	♂ 205.5 (13;13.470)	♂ 160.5 (13; 7.512)	*	*	*
	♀ 171.5 (15; 7.671)	♀ 192.7 (13; 9.936)	♀ 153.2 (17; 6.287)	*	*	*
Length of hind foot	♂ 32.8 (15; 1.781)	♂ 39.1 (13; 1.498)	♂ 30.6 (13; 1.193)	*	*	*
	♀ 31.9 (15; 1.223)	♀ 37.1 (13; 1.256)	♀ 29.5 (17; 1.068)	*	*	*
Length of ear	♂ 6.7 (15; 0.817)	♂ 8.7 (13; 1.932)	♂ 7.0 (13; 0.817)	*	*	*
	♀ 6.5 (15; 0.640)	♀ 7.8 (13; 0.927)	♀ 6.3 (16; 0.577)	*	*	*
Weight	♂ 224.6 (15;22.621)	♂ 350.5 (12;53.490)	♂ 162.0 (13;18.829)	*	*	*
	♀ 179.5 (15;16.961)	♀ 260.8 (13;40.498)	♀ 135.7 (17; 8.394)	*	*	*

[a] Mean values are given with the sample size and standard deviation in parentheses.
* Indicates significant differences ($P < 0.05$).

classified as very slow, less than 0.06 in./hr. (ca. less than 1.5 mm/hr.), slow, 0.06–0.2 in./hr. (ca. 1.5–5.1 mm/hr.), moderately slow, 0.2–0.63 in./hr. (ca. 5.1–16.0 mm/hr.), moderate, 0.63–2.0 in./hr. (ca. 16.0–50.8 mm/hr.), moderately rapid, 2.0–6.3 in./hr. (ca. 50.8–160.0 mm/hr.) and rapid, more than 6.3 in./hr. (ca. more than 160 mm/hr.). These permeability determinations refer to soil water properties and only indirectly to gas diffusion rates.

Numerical data obtained in the course of this study were analyzed statistically to determine significant differences at the 0.05 probability level with a Student-Newman-Keuls *a posteriori* test for multiple comparisons among means (Sokal and Rohlf 1969). Specimens with well-ossified skulls and with all teeth showing at least some wear were considered as adults.

Results and Discussion

Body size relationships

Geomyids have adapted to various soil and substrate conditions with changes in body size and dimensions (Davis 1938, Kennerly 1954). Large individuals are probably more successful in intraspecific interactions (Howard and Childs 1959), whereas smaller species may be better able to occupy less favorable habitats when in competition with a larger form (Kennerly 1959). R. S. Miller (1964) pointed out that larger species tend to be restricted to their preferred soil environments, and larger races and individuals occur in deeper, more tractable soils. However, he concluded that the larger *P. castanops* was competitively inferior to *G. bursarius* in Colorado, indicating that this theory may not always hold.

Data on body size of Geomyidae in northeastern New Mexico are presented in Table 1, along with results of interspecific statistical comparisons between the males and females of the three species. For both sexes the only instance of apparent similarity is in length of tail vertebrae between *P. castanops* and *G. bursarius*. McNab (1966) demonstrated that the vascular tail functions as a thermal regulator.

Interspecific comparisons of males, as well as females, indicate that the three species are significantly different in total length, body length, length of hind foot, length of ear, and weight. Because of the lack of information on behavioral relationships between males and females of each species, interspecific morphological comparisons were made only between the same sexes.

R. S. Miller (1964) found that size differences between *P. castanops* and *G. bursarius* in Colorado were not as marked as between these species and *Thomomys*. Hegdal et al. (1965) reported weights of *P. castanops* from near Carlsbad, New Mexico, to average 248 g for 49 females and 279 g for 11 males. These weights are considerably less than the 260.8 g and 350.5 g, respectively, I recorded. Based on the distribution maps of Russell (1968*b*), the subspecies studied by Hegdal et al. (1965) was *P. c. perplanus* and the populations I studied *P. c. castanops*; this could explain some of the difference in our weights. In northeastern New Mexico *Pappogeomys* weights averaged over 100% more than *Thomomys*, and in excess of 50% more than *Geomys*.

Burrows

Depth.—I noted no differences in the depth from the top of the burrow to the ground surface between *T. bottae* and *P. castanops* burrows, whereas both were significantly shallower than those of *G. bursarius* (Table 2). Since *T. bottae* and *P. castanops* both occurred in fine-textured, rather hard soils and

TABLE 2. Comparisons of burrows and soil preferences between species of pocket gophers[a]

	SPECIES			COMPARISONS		
	(1) *Geomys bursarius*	(2) *Pappogeomys castanops*	(3) *Thomomys bottae*	1 vs. 2	1 vs. 3	2 vs. 3
Burrow depth (mm)	230.201 (40; 111.208)	165.101 (17; 99.697)	131.954 (41; 56.717)	*	*	
Burrow diameter (mm)	78.867 (40; 15.219)	90.018 (17; 12.751)	70.460 (41; 6.624)	*	*	*
Surface soil texture	3.792 (24; 0.932)	2.938 (16; 0.854)	2.546 (22; 0.801)	*	*	
Subsoil texture	3.208 (24; 0.658)	2.813 (16; 0.404)	2.000 (21; 1.095)		*	*
Soil permeability (mm/hr.)	21.463 (21; 47.641)	1.143 (14; 4.250)	2.642 (14; 5.792)	*	*	
Maximum depth of soil (cm)	76.685 (21; 22.021)	53.536 (13; 28.483)	82.550 (12; 21.457)	*		*
Maximum slope of soil surface (%)	4.083 (24; 2.827)	6.625 (16; 3.667)	4.714 (21; 2.704)	*		*

[a] Mean values are given with the sample size and standard deviation in parentheses.
* Indicates significant differences ($P < .05$).

G. bursarius occurred in coarse-textured, sandy soils, the depth of the burrow may be dictated by the texture of the top soil and its insulating properties. The latter two species often were found in close association in the same portion of the study area, subject to the same ambient temperature conditions, but they inhabited soils with different surface textures. Davis et al. (1938) found that a stratum of hard clay limited burrow depth in *Geomys*. Kennerly (1964) suggested gas diffusion rate, which varies with soil moisture and root zone, as a factor limiting burrow depth; M. A. Miller (1957) found saturated soil to be limiting; and Ingles (1949) emphasized water table and frozen soils as factors.

Diameter and shape.—The diameter and shape of the cross-section of burrows were noted at 98 localities. There was a significant difference between the average burrow diameters of *T. bottae*, *G. bursarius*, and *P. castanops* (Table 2). Previous authors (M. A. Miller 1957, Davis et al. 1938, Downhower and Hall 1966, Reichman and Baker 1972) have measured burrow diameters for the three genera of pocket gophers in the United States. M. A. Miller (1957) did not think that body size and burrow diameter were correlated because different individuals occupied a burrow system at different times. It is not known whether this is true for burrows of individuals of a population, but my data (Table 1 and 2) indicate a correlation between the average body size of a species and burrow diameters. This supports previously presented evidence of a positive correlation between burrow diameter and body size of *Geomys* (Kennerly 1954).

Of the *G. bursarius* burrows I studied, 85% (34 of 40) were nearly round in cross-section; the remainder were flattened slightly. The burrow of *G. bursarius* excavated by Smith (1948), was vertically ovoid and slightly larger than the average observed in the current study. For *P. castanops* 77% (13 of 17) of the burrows were round and the remainder were vertically ovoid to irregular in shape. Of the *T. bottae* burrows 76% (31 of 41) were irregularly shaped; many were ovoid and inclined either to the right or left of a vertical axis. This irregular shape was probably due to the loose gravelly composition of the soil in which the species was frequently found. The burrows of the other two species usually occurred in soils free of consolidated particles large enough to cause difficulties in burrowing.

Surface characteristics.—Usually I could easily determine which species was present at any site by observing pecularities of the mounds and other features on the ground surface. Dalquest (1953) noted that *Pappogeomys* mounds in the sandy soils of San Luis Potosí were fewer and larger than those of *Thomomys*. In Union Co. *P. castanops* mounds usually were low and did not appear fresh, although new earthen plugs were often present. Cary (1911) found "characteristic large flat earth heaps" for *P. castanops* in southeastern Colorado. In New Mexico the 25–50 mm high mounds made by *P. castanops* were sometimes difficult to locate, but patches of non-climax vegetation fringing the mounds and feeding area invariably revealed the presence of the species on the shortgrass prairies. Generally, mounds made by *P. castanops* were numerous and concentrated in a restricted area. Long rows of mounds were not found as frequently for *P. castanops* as for the other two species. The result was the appearance of a large area covered with disturbed earth, usually lacking vegetation, with unplugged openings occurring frequently. These open holes were plugged commonly 8–30 cm below the surface opening with soil or large masses of dried grass and feces.

The soil often was honeycombed with burrows 20–60 mm below the surface. These burrows were not connected to the main burrow and most frequently were short and unused. At most of the mound groups at least one or two feces-refuse deposition burrows were found; feces and dried grass were pushed out of the burrow onto the ground surface in a fanwise pattern and the burrow was usually plugged. Previous authors (Tryon 1947, Smith 1948) have noted feces deposits within the burrow systems of *Geomys* and *Thomomys* but a surface deposition has not been described. Hermann (1950) found an abundance of dried grass and feces refuse in abandoned tunnels of *P. castanops* in Texas.

The mounds made by *T. bottae* were generally smaller than those of *G. bursarius*. In the few instances (north of Sofia) where *T. bottae* occurred in sandy soils its mounds were usually two to three times larger, but less numerous than *G. bursarius*. Shallow burrow depth, irregular shape, and small diameter of the burrows usually indicated the presence of *Thomomys* in areas where identification was questionable.

Burrows of all three species were more common in disturbed areas, such as roadways and stream floodplains, than in open climax pastureland. This may be related to the greater diversity of plants in these non-climax areas. Agricultural areas flavored the presence of *G. bursarius* in most areas of the county, but *P. castanops* mounds were numerous in alfalfa fields adjacent to the Cimarron River in northern Union Co. where the other two species did not occur.

Winter activity.—It is well documented that *Thomomys* is active throughout the winter months (Scheffer 1931, Ellison 1946, Tryon 1947, M. A. Miller 1948, Ingles 1949, 1952). Earthen cores made by *Thomomys* were found in the study area following brief periods of snow cover (Snow usually stays on the ground less than 2 weeks in most areas of the county). Downhower and Hall (1966) reported that *G. bursarius* apparently did not make snow cores; however, I found them. Cores were usually 0.5 to 1 m long, often stacked in a criss-cross fashion, and possibly were formed as the pocket gopher pushed freshly excavated earth onto the surface after making short feeding tunnels in the snow. Cores made by *P. castanops* also were observed in the extreme western portion of the study area. These cores were up to 4 m long with frequent branches, and often crossed each other. Their diameter was much greater than those of *Thomomys* or *Geomys*. About one half of their length was composed of semi-circular excavations into the surface of the ground which formed small open "ditches" after the snow had melted. Pockets of dried grass and feces were found in these cores.

Altitude

Union Co. rises more than 960 m in 130 km, sloping from 1,365 m in the southeastern panhandle to more than 2,325 m in the northwest. Altitude affects the size and distribution of *Thomomys* (Grinnell 1926, Davis 1938, Hansen and Bear 1965), as well as influences the separation of *Pappogeomys* from *Thomomys* in Mexico (Davis 1944, Baker 1956) and *Thomomys* from *Geomys* in the United States (Bailey 1926, Jones 1964). This may often be due more to soil differences than the altitudinal changes. Thin, less friable soils usually predominate on higher mountain slopes while deeper soils occur at lower altitudes and in valleys. *G. bursarius* and *P. castanops* occur at similar altitudes throughout Union Co. (mean 1,580 m), whereas *T. bottae* occurs on the average 3,100 m higher. Although there are distinct differences, elevation does not appear to directly affect the distribution of pocket gophers in my study area.

Soils utilized

Surface.—Data from 62 collecting localities revealed that feeding burrows of *T. bottae* and *P. castanops* primarily occurred in loamy-clay-loam surface soils, whereas *G. bursarius* occupied sandy-loam soils (Table 2). Even though the first two species usually were found in diffferent soil associations, both were usually restricted to predominantly clay soils, with *G. bursarius* occupying habitats with sandy soils. The result is an apparently similar soil texture requirement for *Thomomys* and *Pappogeomys*.

Subsoils.—The subsoil texture in which *T. bottae* was found is clay-loam, differing significantly from the other two species (Table 2). Soil analysis from 61 localities also revealed that *P. castanops* and *G. bursarius* occurred on loam to sandy-loam substrates.

Permeability.—*Pappogeomys castanops* and *T. bottae* were not significantly different in occurring in soils of slow to very slow permeability (Table 2). A lime or basalt layer frequently underlay the subsoils where these two species occurred. *Geomys bursarius* occupied soils with moderate permeability, typical of its "preferred" deep, coarse textured, and sandy soil.

Depth.—Analysis of data from 46 localities showed that *P. castanops* occurred in significantly shallower soils than did *T. bottae* or *G. bursarius* (Table 2). The calcareous substratum underlying the soil apparently did not hamper *P. castanops*' ability to survive there.

Slope.—Analysis of data collected at 51 collection

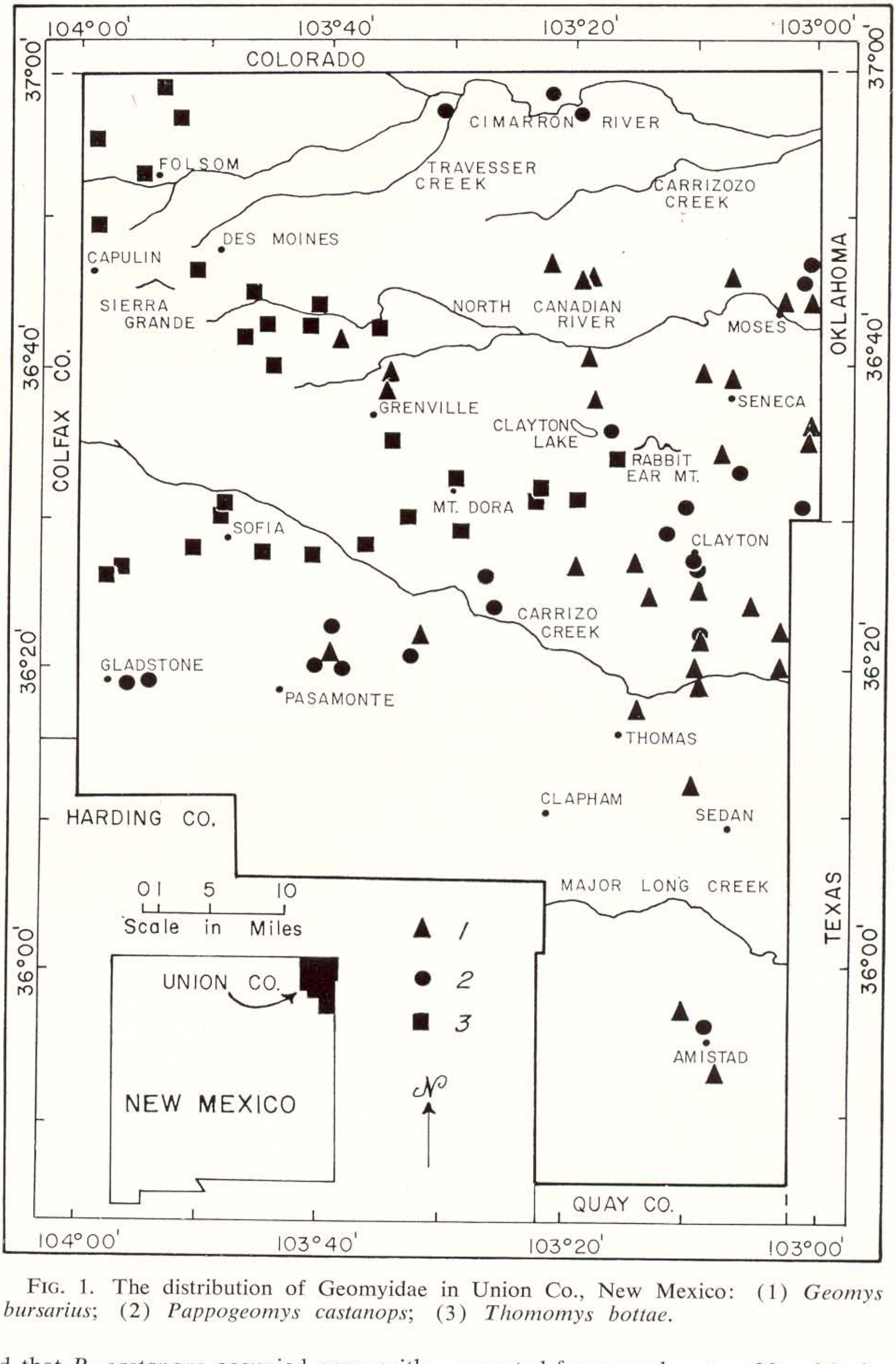

FIG. 1. The distribution of Geomyidae in Union Co., New Mexico: (1) *Geomys bursarius*; (2) *Pappogeomys castanops*; (3) *Thomomys bottae.*

sites indicated that *P. castanops* occupied areas with significantly greater slope than did the other two species (Table 2). It was apparent that *P. castanops* usually occupied hills, not swales, in areas of undulating topography, as well as higher, more sloping areas, where soil was finer textured.

Distribution

Distributions of the three species are shown in Fig. 1. *Geomys bursarius* has not previously been reported from northeastern New Mexico, although it occurs in the central portion of the state as far west as Santa Rosa (Hall and Kelson 1959). Davis (1940*a*) mapped *Geomys* as occurring along the Cimarron River in Union Co., although he reported no specimens from that area. My study indicates that *Geomys* probably has never occurred in that area of New Mexico. Glass reported *P. castanops* from the Black Mesa of Oklahoma (1951*a*) and *G. bursarius* from 12 mi. N Boise City, Cimarron Co., Oklahoma

(1951*b*), about 25 miles east of the Black Mesa. The Cimarron River floodplain provided putatively suitable habitat for *G. bursarius*, but the species apparently has not been able to move upstream along the narrow floodplain between these two localities. The hard soils of the mesa tops also act as a barrier; thus the only large area of suitable soils not occupied by *G. bursarius* in northeastern New Mexico is that of the Cimarron River floodplain. It is doubtful that *G. bursarius* occurs farther west in the county than where I found them (7.3 mi. N, 1 mi. W Grenville, T29N R31E Sec 33, 5,925 ft and 5.2 mi. E, 1.5 mi. N Pasamonte, T24N R31E Sec 5, 5,750 ft).

Pappogeomys castanops has been reported previously from Clayton (Russell 1968*b*). South from the roughed terrain of the Cimarron River drainage and east of Pasamonte and Clapham, *Pappogeomys* is present only in isolated pockets of hard clay-loam soil. The distribution of this species was most striking when observed south of Clayton along New Mexico highway 18, where the topography is low and undulating; *P. castanops* occupied the hill tops and *G. bursarius* the swales and both species occurred as close as 100 m to each other. The distributions of the two forms in this area are an excellent example of geographic sympatry and ecologic allopatry.

Thomomys bottae previously has been reported from Oak Canyon, the mouth of Trinchera Pass, Folsom, and Sierra Grande (Kelson 1951). All of these localities are in the extreme northwest corner of the county. This species reaches the eastern limit of its distribution in New Mexico in Union Co. I never found *Thomomys* within less than a mile of either of the other species. The distribution of *Thomomys* was restricted by basaltic escarpments except where it approached Clayton and Pasamonte and the range of *P. castanops*, and where the two ranges approached each other in the northwestern part of the county along the Cimarron River. Absence of favorable soils did not appear to be a limiting factor in the distribution of *T. bottae*; it may be that it simply has not had time to move farther into these areas. Extensive searching on foot and by automobile revealed no pocket gopher activity and a large gap of 18–20 miles between the ranges of *T. bottae* and *P. castanops* along the Cimarron River.

Conclusions

There was a complex relationship between the three species of pocket gophers studied and the soils they inhabited. The soil environments occupied by each species overlapped, but no two species occurred at the same locality. Possibly interspecific competition has played an important role in determining the distribution, but I feel that it is the result of differential levels of tolerance to soil types among the species. The resulting habitat segregation thus enables all three forms to survive in the same region. These conclusions are based primarily on these findings: *G. bursarius* only in deep sandy soils throughout the county, indicating a narrow range of tolerance; *T. bottae* in a wide range of soils (A test of the mean soil depths indicated no significant difference from *G. bursarius*—Table 2), but most frequently in firm soils with at least some consolidated particles; and *P. castanops* in all major soil types in the county, some, such as the deep sand near the Cimarron River, with apparently more success than others as evidenced by the larger colonies found there. Altitude certainly did not appear to be as important a determinant of pocket gopher distribution as did soils.

In the early Pleistocene *Zygogeomys* probably occurred from the Central Plateau of Mexico over parts of Arizona, Texas, the Oklahoma Panhandle, and most of New Mexico (Russell 1968*a*), including all of the area presently studied. Russell (1968*a*) believed that unsuccessful competition with *Pappogeomys*, and especially *Geomys*, during Irvingtonian time may have extirpated *Zygogeomys* over most of this area; by the late Pleistocene much of the former range of *Zygogeomys* came to be occupied by one or the other of its competitors (i.e., *Pappogeomys* moving northward and *Geomys* westward). Recent fossil evidence from southeastern New Mexico (Harris 1970) indicates a possibility that *Thomomys* was wide spread as late as 12,000–15,000 years ago. To date no fossil data is available for pocket gophers from northeastern New Mexico.

I believe my findings indicate that in the past *Pappogeomys* probably occupied all of Union Co., except for the mountainous northwestern section near Des Moines and Folsom. The disjunct "island-type" of distribution of *Pappogeomys*, which was prominent in the eastern and southern parts of the county, could not have come about by *P. castanops* invading the range of *G. bursarius*. In addition, *G. bursarius* was found in a continuous dendritic distribution pattern narrowing from east to west along areas of favorable soil in association with prominent drainage systems. *Geomys bursarius* has probably reduced the area occupied originally by *P. castanops* within the county, but the relatively strict adherence of *Geomys* to sandy soils enabled *Pappogeomys* to survive at a low density on disjunct islands of hard clay soils. R. S. Miller (1964) checked several localities where *P. castanops* had been collected previously in Colorado and found it to be absent or replaced by *G. bursarius*. *G. bursarius* has possibly displaced both *T. bottae* and *P. castanops* in the deep-soiled valleys in the central section of the county. In most places the area between the ranges of *T. bottae* and *G. bursarius* was occupied by *P. castanops*. From 5 to 25 miles west and northwest of Clayton, *T. bottae* was effectively blocked by the rocky escarpment and the latter two species by differential soil requirements.

The soil requirements of *Pappogeomys* and *Thomomys* in New Mexico are similar since both seem to be limited to firmer soils because of the presence of *G. bursarius*, suggesting the possibility of interspecific competition. During a 2-year period in the Davis Mountains of Texas, Reichman and Baker (1972) found a directional movement of a sympatric area between *Pappogeomys* and *Thomomys* that favored *Pappogeomys*. They postulated this movement was due to the adaptation of *Pappogeomys* to xeric conditions, which enabled this species to use the environment more efficiently. They expressed some doubt about soil's being restrictive since both species were found together in a state of flux; I found no evidence to indicate the forms I studied were in such a state. For this reason I have included a list of collecting localities in the event subsequent investigators may want to revisit collection sites. This has proved to be a valuable tool in the past, as evidenced by R. S. Miller's (1964) and Reichman and Baker's (1972) studies. The current study provides evidence that three genera of pocket gophers that occur in the same general area exhibit habitat segregation and are actually well separated geographically and ecologically by the limits of their individual tolerances.

It is not yet possible to identify precisely the factors operational in separating these fossorial species. Short of actual combat death (if such occurs), physical antagonism would probably result in the loser's retreating to the seclusion of his subterranean retreat. It would be interesting to monitor the activity of pocket gophers in areas where more than one species is likely to occur, and compare the results with similar observations in areas occupied by only one species.

Collecting Localities

Geomys bursarius jugossicularis Hooper. Total, 48, from: 14.8 mi. E, 13.3 mi. N Grenville, T30N R34E Sec 31, 5,420 ft, 2; 3.8 mi. W, 2.6 mi. N Moses, T29N R36E Sec 19, 4,950 ft, 1; 17.2 mi. E, 10.3 mi. N Grenville, T29N R34E Sec 22, 5,250 ft, 1; 18.5 mi. E, 10.3 mi. N Grenville, T29N R34E Sec 23, 5,250 ft, 1; 3.1 mi. E Moses, T29N R37E Sec 32, 4,852 ft, 2; 0.5 mi. W, 0.7 mi. S Moses, T29N R36E Sec 35, 4,780 ft, 1; 7.3 mi. N, 1 mi. W Grenville, T29N R31E Sec 33, 5,925 ft, 1; 10 mi. E, 10.5 mi. N Mt. Dora, T28N R34E Sec 16, 5,200 ft, 1; 2 mi. E, 4.7 mi. N Grenville, T28N R32E Sec 18, 5,800 ft, 3; 2 mi. N, 3.4 mi. W. Seneca, T28N R35E Sec 22, 5,000 ft, 2; 0.7 mi. N Seneca, T28N R36E Sec 29, 4,900 ft, 1; 1.5 mi. E, 1.3 mi. N Grenville, T27N R31E Sec 1, 5,800 ft, 4; 10.2 mi. E, 5.9 mi. N Mt. Dora, T27N R34E Sec 4, 5,300 ft, 2; 10.1 mi. E, 7.9 mi. N Clayton, T27N R37E Sec 5, 4,765 ft, 1; 4 mi. S, 1.1 mi. W Seneca, T27N R35E Sec 13, 4,850 ft, 1; 10 mi. E, 5.7 mi. N Clayton, T27N R37E Sec 20, 4,700 ft, 2; 2 mi. S, 9.3 mi. W Clayton, T25N R34E Sec 7, 5,200 ft, 1; 4.8 mi. W, 1.8 mi. S Clayton, T25N R34E Sec 12, 5,050 ft, 2; 4.8 mi. S, 3.7 mi. W Clayton, T25N R34E Sec 24, 5,050 ft, 1; 5.5 mi. S Clayton, T25N R35E Sec 26, 4,900 ft, 1; 6.8 mi. S, 4¼ mi. E Clayton, T25N R36E Sec 32, 4,800 ft, 1; 5.2 mi. E, 1.5 mi. N Pasamonte, T24N R31E Sec 5, 5,750 ft, 1; 2.2 mi. N, 12.8 mi. E Pasamonte, T24N R32E Sec 2, 4,900 ft, 2; 7.8 mi. E, 9.1 mi. S Clayton, T24N R36E Sec 13, 4,620 ft, 2; 10.1 mi. S Clayton, T24N R35E Sec 27, 4,840 ft, 1; 1 mi. E, 1 mi. N Thomas, T24N R34E Sec 36, 4,950 ft, 2; 13.5 mi. S Clayton, T23N R35E Sec 10, 4,800 ft, 1; 14.6 mi. S Clayton, T23N R35E Sec 10, 4,800 ft, 2; 4.9 mi. E, 6 mi. N Sedan, T22N R36E Sec 12, 4,550 ft, 1; 3 mi. W, 1.6 mi. N Sedan, T22N R35E Sec 3, 4,700 ft, 1; 2.4 mi. W, 3.2 mi. N Amistad, T20N R35E Sec 10, 4,600 ft, 1; and 0.4 mi. W, 3.7 mi. S Amistad, T19N R36E Sec 19, 4,400 ft, 2.

Pappogeomys castanops Baird. Total, 33, from: Pepper Ranch, 9 mi. N, 34 mi. E Folsom, T32N R34E Sec 33, 4,700 ft, 1; 0.9 mi. E, 29.5 mi. N Mt. Dora, T32N R33E Sec 31, 5,000 ft, 1; 33 mi. N, 6.3 mi. W Clayton, T31N R34E Sec 2, 5,200 ft, 1; 2.6 mi. E, 6 mi. N Moses, T30N R37E Sec 32, 4,800 ft, 1; 2.2 mi. E, 3.3 mi. N Moses, T29N R37E Sec 18, 4,800 ft, 1; 0.5 mi. E Clayton Lake, T27N R34E Sec 14, 5,100 ft, 1; 3.5 mi. E, 6.5 mi. N Clayton, T27N R36E Sec 30, 5,000 ft, 3; 9 mi. E, 4.1 mi. N Clayton, T26N R37E Sec 7, 4,700 ft, 3; 2.9 mi. N, 1.7 mi. W Clayton, T26N R35E Sec 16, 5,000 ft, 1; 2.3 mi. W, 1.1 mi. N Clayton, T26N R35E Sec 20, 5,100 ft, 1; ¼ mi. S Clayton, T26N R35E Sec 35, 5,050 ft, 1; ½ mi. S Clayton, T25N R35E Sec 2, 5,050 ft, 3; 6.6 mi. S, 3.5 mi. E Mt. Dora, T25N R33E Sec 9, 5,300 ft, 2; 5.2 mi. E, 4.5 mi. N Pasamonte, T25N R31E Sec 20, 5,850 ft, 1; 12.9 mi. W, 4.9 mi. S Clayton, T25N R33E Sec 22, 5,400 ft, 2; 17.3 mi. W, 7.4 mi. S Clayton, T24N R32E Sec 3, 5,500 ft, 2; 1.2 mi. N, 3.6 mi. E Pasamonte, T24N R31E Sec 7, 5,800 ft, 1; 1.2 mi. N, 7.2 mi. E Pasamonte, T24N R31E Sec 10, 5,700 ft, 1; 1.2 mi. E Gladstone, T24N R28E Sec 22, 5,900 ft, 2; 2.2 mi. E Gladstone, T24N R28E Sec 23, 5,900 ft, 1; 9.7 mi. S Clayton, T24N R35E Sec 15, 4,860 ft, 2; and 0.5 mi. W, 0.6 mi. N Amistad, T20N R35E Sec 36, 4,500 ft, 1.

Thomomys bottae cultellus Kelson. Total, 46, from: 9 mi. N, 2 mi. E Folsom, T32N R29E Sec 30, 6,480 ft, 3; 3.3 mi. E, 3.6 mi. N Folsom, T31N R29E Sec 28, 6,000 ft, 1; 2.7 mi. W, 1.4 mi. N Folsom, T30N R28E Sec 4, 6,600 ft, 2; 0.8 mi. W, 0.4 mi. S

Folsom, T30N R28E Sec 14, 6,500 ft, 2; 3.2 mi. N, 0.9 mi. E Capulin, T30N R28E Sec 32, 7,800 ft, 3; 1.7 mi. W Des Moines, T29N R29E Sec 8, 6,750 ft, 2; 3.5 mi. E, 1.4 mi. S Des Moines, T29N R30E Sec 20, 6,300 ft, 1; 10.3 mi. E, 2.4 mi. S Des Moines, T29N R31E Sec 29, 6,000 ft, 2; 2 mi. E, 8.8 mi. N Grenville, T29N R32E Sec 30, 5,800 ft, 2; 8.7 mi. E, 4.5 mi. S Des Moines, T28N R31E Sec 6, 6,100 ft, 1; 5.1 mi. E, 4.5 mi. S Des Moines, T29N R30E Sec 33, 6,250 ft, 2; 5.6 mi. S, 2.3 mi. E Des Moines, T28N R30E Sec 7, 6,400 ft, 1; 6.3 mi. W, 2.2 mi. N Grenville, T28N R30E Sec 27, 6,350 ft, 4; 2 mi. S, 1.2 mi. E Grenville, T27N R31E Sec 13, 5,900 ft, 2; 5.1 mi. W, 5.9 mi. N Clayton, T27N R34E Sec 35, 5,450 ft, 1; Mt. Dora, T26N R32E Sec 1, 5,750 ft, 2; 6 mi. E, 1.5 mi. S Mt. Dora, T26N R33E Sec 11, 5,450 ft, 1; 5.8 mi. E, 1.7 mi. S Mt. Dora, T26N R33E Sec 11, 5,400 ft, 1; 7.6 mi. W, 2.4 mi. N Clayton, T26N R34E Sec 16, 5,300 ft, 1; 2.8 mi. N Sofia, T26N R29E Sec 15, 6,380 ft, 1; 2 mi. N Sofia, T26N R29E Sec 22, 6,350 ft, 2; 5.3 mi. W, 2.5 mi. S Mt. Dora, T26N R31E Sec 24, 5,800 ft, 1; 1.7 mi. W Sofia, T26N R29E Sec 28, 6,300 ft, 2; 1.8 mi. E Sofia, T26N R29E Sec 25, 6,180 ft, 1; 10.2 mi. E Sofia, T26N R31E Sec 28, 5,950 ft, 1; 5.5 mi. E Sofia, T26N R30E Sec 34, 6,080 ft, 1; 4.3 mi. S Mt. Dora, T26N R32E Sec 26, 5,500 ft, 1; 8.6 mi. N, 1 mi. E Gladstone, T25N R28E Sec 4, 6,100 ft, 1; and 6.1 mi. N Gladstone, T25N R28E Sec 17, 6,100 ft, 1.

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