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EFFECTS OF SPECIES, SEX, AGE, AND HABITAT ON GEOMETRY OF POCKET GOPHER FORAGING TUNNELS

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Home-range size and shape are influenced by cost–benefit relationships associated with acquiring resources. Subterranean animals may be particularly affected by food availability and soil conditions because of the close coupling of their activity to soil and the high energetic expense of digging. We examined foraging tunnel length, area, and geometry (e.g., number of branches and turning angles) of 3 species of pocket gophers (*Geomys attwateri*, *Geomys bursarius*, and *Thomomys bottae*) in their natural habitats, which differed in food abundance and soil characteristics. Burrow features (except length and area) were similar among species, sexes, ages, and habitats. However, burrows of adults were longer and occupied larger areas than those of juveniles, and burrow system length and area decreased with increasing vegetation biomass and with increasing soil clay content of soil (i.e., increasing expense of digging). Our findings reveal common patterns of burrow geometry, which suggest that there may be an underlying strategy defining geometric features of burrows within this family of subterranean rodents.

Key words: burrowing patterns, energetics, Geomyidae, home range, soil, subterranean, vegetation

Home-range size and shape are functions of cost–benefit considerations based on resource acquisition and use of space for garnering resources (often food, also mates). An animal must maintain a net energy gain from the costs of seeking and acquiring resources and resource returns. Moreover, an animal can optimize energetic considerations by establishing a home range and foraging in a resource-rich area (Schoener 1971; Stephens 1986) or adjusting home-range configuration to maximize energy gain (Carpenter et al. 1983).

Establishing a home range in a resource-rich location is a particularly challenging task for animals that cannot detect resources from a distance. For example, subterranean rodents are limited in their ability to detect food through the soil (Benedix 1993). Additionally, the energetic cost of excavating a burrow is 360–3,400 times the cost of walking a similar distance aboveground (Vleck 1979). As a consequence, there should be significant selective pressure on subterranean mammals to excavate their burrows in optimal configurations.

Pocket gophers (Geomyidae) are subterranean rodents whose burrowing patterns are affected by their solitary social system (Reichman et al. 1982) and their need to acquire food (Andersen 1988, 1990). Each individual constructs a burrow that serves as its home range (Miller and Bond 1960). Pocket gophers forage for plant material and seek mates by extending their burrows within a relatively fixed area (Reichman et al. 1982). They spend their lives belowground (except during dispersal), and thus burrow location and configuration of shallow tunnels for foraging (‘‘foraging tunnels’’) are critical for resource acquisition. Spatial configurations of burrows serve as snapshots of the movement paths of pocket gophers at any one time and thus can yield information about their burrowing patterns as they search for resources.

We examined foraging tunnel size and geometry (e.g., number of branches and turning angles) of pocket gophers by using burrow maps and site data from previous studies. We analyzed the foraging tunnels (hereafter referred to as ‘‘burrows’’ for simplicity) of 3 species of pocket gophers, *Geomys attwateri*, *Geomys bursarius*, and *Thomomys bottae*, each at 2 sites differing in food abundance and soil conditions. The 3 species differed in body size, and hence in physiological demands. We examined whether burrow geometry was species-specific and how geometry was affected by food availability, soil conditions, age, and sex. We made 2 sets of predictions. First, assuming

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TABLE 1.—Site locations, body masses of animals, and vegetation and soil characteristics. Vegetation biomass before conversion ("original") is given, and converted ("total") above- and belowground biomass (conversion performed where only aboveground biomass was given by existing studies). Where body masses or soil data were not recorded at a site, data are presented from other sources in the literature.

		Biomass of vegetation (g/m^2)			
Location	Body mass, $\bar{X}$	Total, $\bar{X}$ (n)	Original, $\bar{X}$ ± SE	Sand (%), $\bar{X}$	Clay (%), $\bar{X}$
Geomys attwateri					
Venado Sands, Texas	132.3	109 (30)	95 ± 18	>91	1.4
Lake Trap, Texas	148.9	215 (30)	188 ± 24	>91	4.1
G. bursarius					
Konza, Kansas	185[a]	2,069 (42)	658 ± 25	7.7[b]	28.3[b]
Cedar Creek, Minnesota	185[a]	307 (64)	97 ± 24	90[c]	4.7[c]
Thomomys bottae					
Tuzigoot Monument, Arizona	121.3	1,421 (20)	1,421 ± 116	54[d]	23[d]
Museum of N. Arizona, Arizona	121.3[e]	757 (20)	757 ± 123	No data	36.5[f]

[a] Ruff and Wilson 1999.
[b] Knapp 1998.
[c] Grigal et al. 1974.
[d] United States Geological Survey 2000.
[e] Reichman et al. 1982.
[f] United States Department of Agriculture 1975.

equal net energy gain per meter of burrow excavated, we predicted the following: (1) Species with the largest body mass will have the largest burrow systems (i.e., greatest length and area) to acquire sufficient food to meet their energetic needs (McNab 1963). (2) Males will have larger burrows than those of females because males have a larger body mass, and because they search for mates (Bandoli 1981; Reichman et al. 1982). (3) Adults will have larger burrows than those of juveniles because adults have a larger body mass. Second, assuming variable net energy gain per meter of burrow excavated, we also predicted: (4) Burrows will be shorter in areas of high vegetation abundance because net energy gain per meter of burrow dug will be greater than in areas of low vegetation abundance (all else being equal). (5) Burrows will be shorter in areas of sandy soils because net energy gain per meter of burrow dug will be greater than in areas of clay soils because of the lower cost of digging in sand (all else being equal—Vleck 1979).

Although belowground behavior of subterranean rodents is difficult to assess, they maintain a dynamic equilibrium with regard to burrow length (Andersen 1987; Zinnel 1992). Seasonally, burrow length may vary as individuals refill old burrow sections rather than depositing excavated soil on the surface (Crouch 1933; Sparks and Andersen 1988; Sumbera et al. 2003). The specific geometry of individual burrows is also dynamic, changing through time as the resident excavates new tunnels for foraging, or when a vacant system is taken over by a new resident, which happens within minutes to a few days (Reichman et al. 1982; Zinnel and Tester 1994). Burrows examined in this study were mature burrow systems (i.e., the products of at least 1 season of pocket gopher excavation). Although home-range size and structure can vary over time, for pocket gophers in particular, Reichman et al. (1982) present internal burrow geometry, interburrow spacing, and population density data that suggest stability in burrow configurations in mature populations. Therefore, we assumed that burrow configurations were stable and could be attributed to the inhabitant at the time of burrow mapping.

MATERIALS AND METHODS

Species and sites.—We analyzed burrows at 2 sites for 3 species of pocket gophers, *G. attwateri*, *G. bursarius*, and *T. bottae* (Table 1). All burrow system maps were taken from previous studies, which differed in foci and details and spanned 13 years of data collection. We used burrow maps from 2 Arizona sites, Tuzigoot Monument and Museum of N. Arizona (Reichman et al. 1982); 2 Texas sites, Venado Sands and Lake Trap (Cameron et al. 1988); 1 Minnesota site, Cedar Creek (Wasley 1995); and 1 Kansas site, Konza (W. E. Rogers, in litt.). Sex and age (categorized either as adult or juvenile based on reproductive maturity, body mass, or both, depending on methods of the existing studies) data were available for 3 sites (*G. attwateri*, Venado Sands and Lake Trap; *T. bottae*, Tuzigoot Monument), only sex data was available for 1 site (*G. bursarius*, Cedar Creek), and neither was available for the other 2 sites (*G. bursarius*, Konza; *T. bottae*, Museum of N. Arizona).

Data on standing crop of vegetation were taken at each site at the time of burrow mapping. At 4 of the 6 sites, only aboveground biomass was measured; at the other 2 sites combined above- and belowground biomass was measured (Table 1). For sites where only aboveground biomass data were recorded, we extrapolated belowground biomass by using root-to-shoot ratios (Andersen and MacMahon 1981). Percentage sand and clay in the soil was measured directly at 2 sites and extracted from published records for the remaining 4 sites (Table 1).

Both sites where *G. attwateri* occurred were characterized by low vegetation biomass and sandy soils. *G. attwateri* was intermediate in size to *G. bursarius* and *T. bottae*.

The 2 sites for *G. bursarius* differed in their habitat characteristics. Konza had the highest vegetation biomass of all sites examined as well as high soil clay content. Cedar Creek was characterized by low vegetation biomass and sandy soils. *G. bursarius* had the largest body mass of the 3 species.

Both sites where *T. bottae* occurred had high vegetation biomass and high soil clay content.

Burrow measurements.—Burrows ranged in size and structural complexity (see Reichman et al. [1982] for example illustrations of burrow systems). We digitized burrow maps, and then, by using the imaging program SigmaScan (SPSS 1996), we measured several major burrow features (Romañach and Le Comber 2004; Fig. 1), including number of branches; length of each segment (nonterminal burrow sections) and each branch (terminal burrow section); total length of burrow system (i.e., sum of all segment and branch lengths); branch and turn angles; linearity of each segment and each branch (i.e., displacement from a straight line); area occupied by burrow system (convex polygon drawn around burrow system); and shape of burrow system (calculated by using SigmaScan; unitless measure defined as $4\pi(\text{area})/\text{perimeter}^2$, which is an index of the circularity of an object, where shape ranges from 0 [= straight line] to 1 [= circle]).

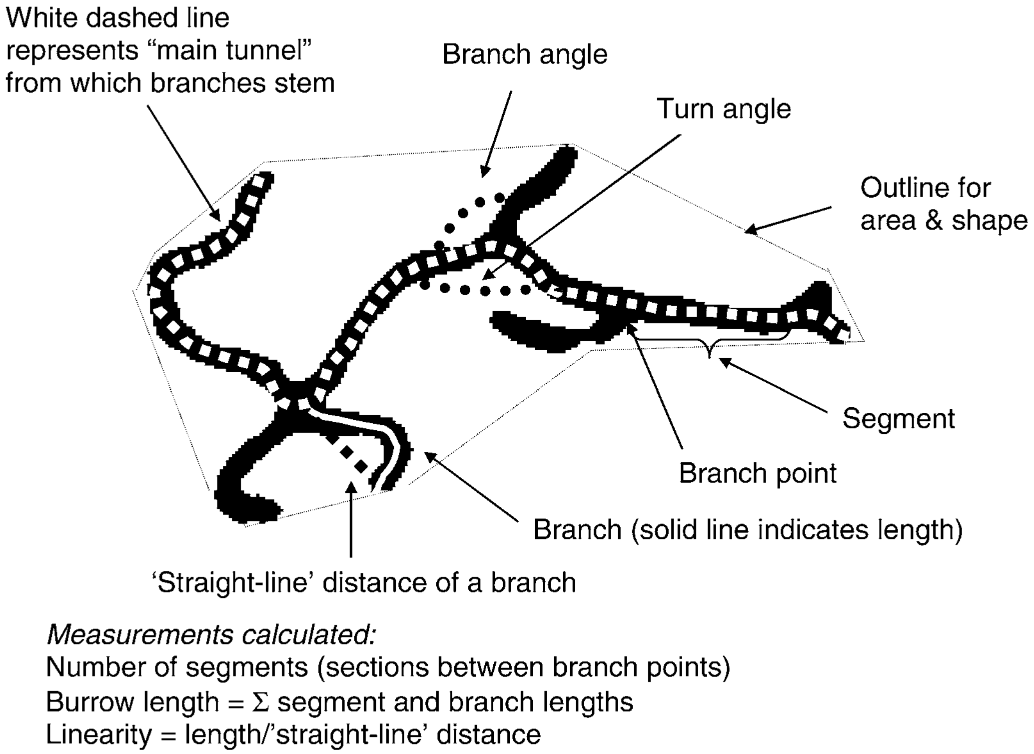

FIG. 1.—Sample burrow system of *Thomomys bottae* showing geometric measurements.

Statistics.—We analyzed data by using SAS statistical software (SAS Institute Inc. 1989). We used 1-way analysis of variance to examine differences in burrow system geometry among species and between ages (only 1 species had data from adults and juveniles; see "Results") based on general linear models that included all burrow geometry metrics. Shape data were arcsine transformed before performing analyses (Zar 1999). We used analysis of covariance (with species as a factor) to examine differences in burrow system geometry between sexes.

Each of the 6 sites had a single measure of vegetation biomass and soil clay content. Therefore, we calculated average burrow system metrics for each site and used these averages to perform separate, simple linear regressions with vegetation abundance and soil type. Percent clay content data were arcsine transformed before performing analyses.

RESULTS

All internal geometric features were statistically indistinguishable ($P > 0.05$ for each metric) among burrow systems from all sites (Table 2). This result may indicate that variation in these metrics is controlled by factors that we did not consider in our study (e.g., population density and habitat variability) or that burrow geometry has little variability across all sites. To

TABLE 2.—Burrow geometry data (mean ± *SE*) for each species at each site. Significant differences ($P < 0.05$) among species for length and area are indicated by different superscript letters. (Our measure of total burrow length at the Museum of N. Arizona site is a corrected value from Reichman et al. [1982].)

	No. burrows	No. branches	Segment length (m)	Total length (m)	Area (m^2)	Turn angle (°)	Branch angle (°)	Shape	Linearity
Geomys attwateri									
Venado Sands	6	16.0 ± 2.8	3.1 ± 0.3	91.9 ± 22.4^a	499.1 ± 320.9^a	144.6 ± 1.7	127.0 ± 3.6	0.67 ± 0.1	1.3 ± 0.0
Lake Trap	4	24.5 ± 4.6	2.5 ± 0.6	109.4 ± 31.6^a	431.1 ± 189.6^a	145.3 ± 6.1	124.9 ± 6.3	0.68 ± 0.0	1.3 ± 0.0
G. bursarius									
Konza	38	6.7 ± 1.4	2.0 ± 0.2	23.1 ± 4.5^b	34.5 ± 10.2^b	144.4 ± 4.2	129.8 ± 2.7	0.54 ± 0.0	1.5 ± 0.1
Cedar Creek	20	11.6 ± 2.5	2.5 ± 0.2	51.8 ± 11.7^b	95.3 ± 28.6^b	137.7 ± 3.5	134.2 ± 2.9	0.64 ± 0.0	1.5 ± 0.1
Thomomys bottae									
Tuzigoot Monument	25	13.7 ± 2.4	1.4 ± 0.1	33.6 ± 5.1^b	41.5 ± 8.2^b	141.5 ± 2.2	123.3 ± 1.8	0.58 ± 0.0	1.2 ± 0.0
Museum of N. Arizona	19	16.1 ± 2.7	1.1 ± 0.1	33.7 ± 5.0^b	38.48 ± 8.6^b	141.9 ± 1.3	126.2 ± 1.0	0.60 ± 0.0	1.3 ± 0.0

Table 3.—Burrow geometry data (mean ± *SE*) by sex for all species combined, with data from Venado Sands, Lake Trap, Cedar Creek, and Tuzigoot Monument. Burrow geometry data (mean ± *SE*) by sex and age (adult and juvenile) for *Thomomys bottae*, with only data from Tuzigoot Monument. Significant differences ($P < 0.05$) among sex and age classes are shown by different superscript letters.

		No. burrows	No. branches	Segment length (m)	Total length (m)	Area (m^2)	Turn angle (°)	Branch angle (°)	Shape	Linearity
Geomys attwateri, *G. bursarius*, and *Thomomys bottae*	Female	22	12.1 ± 2.3	2.0 ± 0.2	42.1 ± 8.6	174.4 ± 87.4	142.7 ± 2.3	126.2 ± 1.8	0.6 ± 0.0	1.3 ± 0.0
	Male	19	14.9 ± 2.8	1.8 ± 0.2	49.6 ± 10.8	83.3 ± 26.9	143.5 ± 2.7	122.1 ± 2.3	0.6 ± 0.0	1.3 ± 0.0
T. bottae	Adult female	9	15.1 ± 4.6	1.3 ± 0.1	31.5 ± 5.1^{a}	33.1 ± 5.4^{a}	138.3 ± 3.3	128.6 ± 2.6	0.6 ± 0.0	1.2 ± 0.0
	Adult male	6	20.5 ± 6.3	1.9 ± 0.2	61.2 ± 13.9^{b}	96.4 ± 20.2^{b}	149.6 ± 3.4	116.3 ± 3.1	0.5 ± 0.0	1.2 ± 0.0
	Juvenile female	4	9.3 ± 3.5	1.5 ± 0.2	24.4 ± 6.5^{a}	23.6 ± 7.3^{a}	144.4 ± 4.3	119.3 ± 1.0	0.6 ± 0.1	1.3 ± 0.0
	Juvenile male	6	7.8 ± 1.8	1.0 ± 0.1	15.3 ± 2.8^{c}	11.1 ± 2.7^{c}	135.3 ± 6.0	125.3 ± 4.4	0.6 ± 0.1	1.2 ± 0.0

distinguish between these 2 possibilities, we calculated the coefficient of variation (CV) for each metric to determine the degree of variability within each of them. Number of branches and segment length had the highest variation ($CV = 0.40$ and 0.36, respectively). In contrast, angular measurements showed remarkably little variation across sites ($CV = 0.02$–0.03). Shape and linearity were intermediate in variability (each with $CV = 0.09$).

Total length and area of burrow systems showed significant differences across species, sexes, ages, vegetation abundances, and soil characteristics (Tables 2 and 3), so these results will be presented in detail.

Species.—The intermediate-sized species, *G. attwateri*, had burrows that were longest ($F = 14.9$, $d.f. = 2$, $P \ll 0.01$) and that occupied the largest area ($F = 25.79$, $d.f. = 2$, $P = 0.01$). Total burrow length ($F = 0.66$, $d.f. = 1$, $P = 0.42$) and burrow system area ($F = 0.97$, $d.f. = 1$, $P = 0.33$) did not differ between the largest and smallest species, *G. bursarius* and *T. bottae*, respectively.

Sex and age.—Four sites had data on the sex of the individual occupying each burrow, including data from at least 1 site for each species (Table 1). No difference was found in total burrow length between females and males ($F = 0.56$, $d.f. = 1$, $P = 0.46$; Table 3). Area of burrow systems also did not differ between females and males ($F = 1.10$, $d.f. = 1$, $P = 0.30$).

Of the 3 sites with data on age of occupant, only 1 site (*T. bottae*, Tuzigoot Monument site) had both adults and juveniles present (other sites had only adults). Burrows of adult *T. bottae* at Tuzigoot were longer ($F = 10.10$, $d.f. = 1$, $P < 0.01$) and occupied larger areas ($F = 17.93$, $d.f. = 1$, $P < 0.01$) than burrows of juveniles. A sex-by-age interaction ($F = 5.42$, $d.f. = 1$, $P = 0.03$; Table 3) was found for burrow length; adult males had longer burrows than did juvenile males ($P < 0.01$). Adult and juvenile females had similar burrow lengths ($P = 0.56$), and their burrows were intermediate in length to those of adult and juvenile males. The same sex-by-age interaction pattern described for burrow length was found for burrow system area ($F = 11.45$, $d.f. = 1$, $P < 0.01$; Table 3).

Vegetation biomass.—Total burrow length decreased ($r^2 = 0.62$, $d.f. = 1$, $P = 0.06$) and burrow system area decreased ($r^2 = 0.49$, $d.f. = 1$, $P = 0.12$; Figs. 2A and 2B) with increasing vegetation biomass across all sites. We examined trends within species although we had only 2 sites per species. Burrow systems of *G. attwateri* were longer and occupied smaller areas at the site with high biomass compared to burrows at the site with low biomass. For *G. bursarius*, burrow systems were shorter and occupied smaller areas at the site with high biomass compared to burrows at the site with low biomass. For *T. bottae*, burrows were shorter and occupied larger areas at the site with high biomass compared to burrows at the site with low biomass.

A combination of the aforementioned length and area results have the potential to reveal burrow system shape; however, a multiple regression ($r^2 = 0.11$, $d.f. = 3$, $P \ll 0.01$) showed that although shape was correlated with total burrow length ($F = 6.74$, $d.f. = 1$, $P = 0.01$), shape was not affected by burrow system area ($F = 1.14$, $d.f. = 1$, $P = 0.29$) nor an interaction between length and area ($F = 1.04$, $d.f. = 1$, $P = 0.31$).

Soil characteristics.—Total burrow length decreased ($r^2 = 0.70$, $d.f. = 1$, $P = 0.04$) and burrow system area decreased ($r^2 = 0.67$, $d.f. = 1$, $P = 0.05$) as soil clay content increased (Figs. 2C and 2D). We examined trends within species although we had only 2 sites per species. For *G. attwateri*, burrow systems were longer and occupied smaller areas at the site with soil of high-clay content compared to burrows from the site with soil of low-clay content. For *G. bursarius*, burrows were shorter and occupied smaller areas at the high-clay site compared to burrows at the low-clay site. For *T. bottae*, burrow systems were longer and occupied smaller areas at the high-clay site compared to burrows at the low-clay site.

A linear regression of vegetation biomass and soil clay content showed increasing vegetation biomass with increasing clay ($r^2 = 0.57$, $d.f. = 1$, $P = 0.08$).

Discussion

Two predictions regarding burrow system size (length and area) were met. Burrow systems of adults were larger than those of juveniles (prediction 3), and, in general (across species), burrow system size decreased with increasing vegetation biomass (prediction 4). However, 3 predictions were not met: (prediction 1) the species with the largest body size did not have the largest burrow systems; (prediction 2) on average, males did not have larger burrow systems than females (consistent with findings of Sumbera et al. [2003] for a bathyergid species); and (prediction 5) burrow system size decreased with increasing clay content of soil. The intermediate-sized species, *G.*

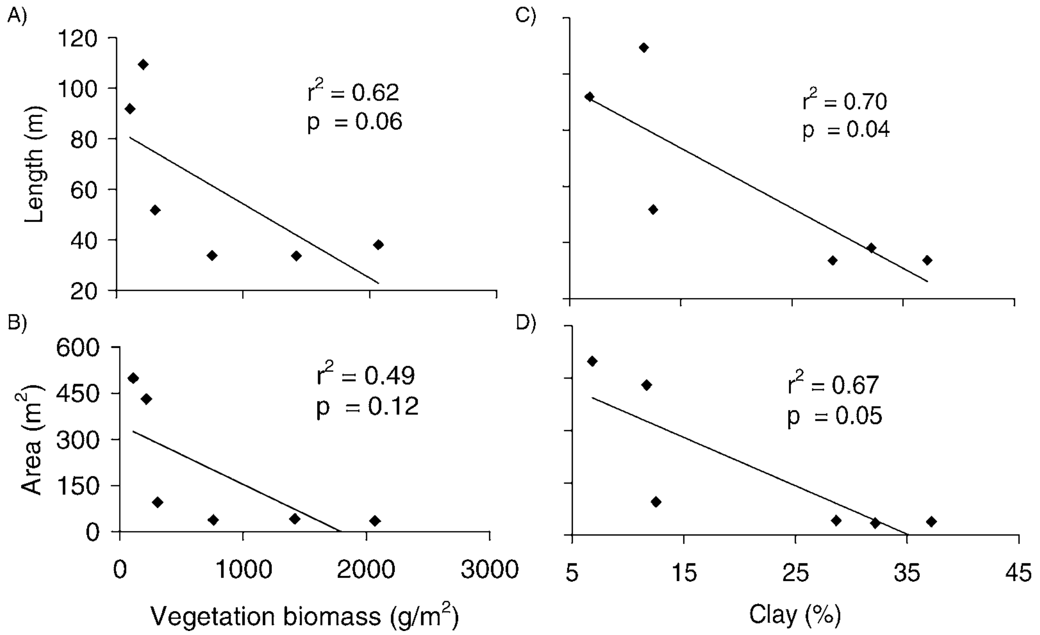

FIG. 2.—Relationship between vegetation biomass and A) total burrow length and B) burrow system area, and between soil clay content and C) total burrow length and D) burrow system area, for all species (*Geomys attwateri*, *G. bursarius*, and *Thomomys bottae*) across all sites.

attwateri, had the largest burrow systems, likely because it occurred in areas with sandy soils (i.e., low digging cost) and low food availability. Females had equivalent sizes of burrow systems (length and area) to males, although their body mass was lower, possibly the burrow size is a result of the need by females to obtain sufficient food particularly during pregnancy and lactation (Hickman 1990). Burrows were largest in sandy soils, which were those inhabited by *G. attwateri* (as noted above).

Burrow system size across species decreased with increasing vegetation biomass and soil clay content. However, we had burrow maps at only 2 sites for each species, and because these sites differed in their habitat characteristics, we were limited in our ability to detect intraspecific burrowing patterns among habitat types. Thus, a larger sample size across many habitat types would be required to fully examine intraspecific burrowing patterns.

Burrow geometry (excluding length and area) was similar across species, sex, age, and habitat, suggesting that internal burrow geometry might be the outcome of a burrowing strategy common to geomyids. All subterranean rodents have common influences of life belowground (e.g., high energetic cost of digging and foraging method), which could result in an optimal burrow configuration, perhaps for the most energetically efficient configuration. For example, Vleck (1981) found an energetically optimal segment length for 1 geomyid species, Andersen (1988) found an optimal turning angle for the geomyid species that he examined, and Sumbera et al. (2003) suggested that burrow configurations reflected energetic considerations (e.g., soil excavation costs) for a bathyergid species. In our study, internal geometry appeared to be consistent across species and habitats. Burrow system sizes were adjusted based on energetic costs and rewards in accordance with food availability and soil type, consistent with findings of previous studies (Reichman et al. 1982; Seabloom and Reichman 2001).

Our findings on internal geometry also were consistent with previous findings reported in the literature. Andersen (1988) found that average "directionality" of a burrow (i.e., deviation from a straight line) for *G. bursarius* was 46.5°. When we converted our turn angle metric into Andersen's directionality metric (180° minus the turn angle), we found an average directionality across sites and species of 37.4°. Additionally, Andersen (1988) measured "branching angles" and found an average of 80° for *G. bursarius*. When using Andersen's metric, our average branching angle (360° minus the turn angle and branch angle) was 89.9°. Because of differences in the ways in which burrows were mapped, we were unable to compare our segment lengths to those in the published literature.

Our results showed that segment length and number of branches, although statistically indistinguishable across sites, were much more variable than were angular measurements. This suggests that the ability of pocket gophers to alter their foraging behavior relies primarily on changes in the overall size of the burrows and to a lesser degree on the size of other components (e.g., segment length). In contrast, the angular components of the burrow appear to be highly constrained, perhaps by energetic constraints that are common to all geomyids (Andersen 1988). The similarities between our angular measurements and those of Andersen (1988) strengthen our suggestion for the existence of common burrowing patterns within geomyids.

We were unable to disentangle the relationship between vegetation biomass and soil clay content. However, previous modeling work examining the energetics of burrowing by pocket gophers revealed that vegetation biomass and digging strategy (when using area-restricted searching) were the most important factors contributing to burrow geometry, with little or no effect of soil clay content (Romañach 2003). The model showed that caloric value of vegetation was sufficient to compensate for the cost of digging, even in the most energetically demanding soils.

Additionally, Romañach (2003) compared model results to existing field data and suggested that animals in their natural environments may use area-restricted searching (i.e., concentrating foraging effort in food-rich patches once they are encountered). Thus, it is likely that burrowing patterns revealed by our current study were driven by food availability rather than by digging cost.

One of our results was inexplicable based on energetic predictions. Both sites occupied by *T. bottae* had similar soil clay content, but 1 site contained twice as much vegetation (Table 1). Energetic gain per meter of burrow dug should be higher at the site with high vegetation biomass than at the site with low biomass, thus we predicted (prediction 4) smaller burrow systems at the site with high biomass. Instead, we found similar burrow sizes for *T. bottae* at both sites (Table 2). Both sites had uniform vegetation and soil features (Reichman et al. 1982), therefore we do not expect within-site spatial variation in these factors to have played a major role. This similarity in burrow sizes suggests that factors not considered in our study, such as social behavior associated with mate choice or adequate burrow size for gas exchange (Kennerly 1964), may favor a larger burrow size than that predicted by energetics alone.

Influences on pocket gopher burrow length, area, and internal geometry are more than those considered in our study. When animals dig a burrow, their burrowing patterns can be affected by additional physical considerations such as hillslope angle (Seabloom et al. 2000) and needs for respiratory gas exchange (Wilson and Kilgore 1978), and likely also features such as soil irregularities and vegetation type. The aforementioned factors may contribute to adjustments animals make in burrow location, length, internal geometry, and depth. However, we did not consider these factors in our study because, within each site, areas occupied by burrows were fairly uniform with respect to these physical features. Future work examining these factors could reveal their relative importance in the determination of burrow size, shape, and structure.

In a widespread family such as Geomyidae, to study burrows by excavating a large sample of burrows in the diversity of habitats (across thousands of kilometers) in which they occur is impractical. Thus, we used as many previously excavated burrow maps as were available across a range of habitat types to examine burrowing patterns. Even with the limited information we were able to synthesize, our results suggest that there is a common burrowing pattern within this family of subterranean rodents. If this is so, studies of distantly related ecological cognates on other continents are warranted to determine whether these patterns are characteristic of subterranean rodents.

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