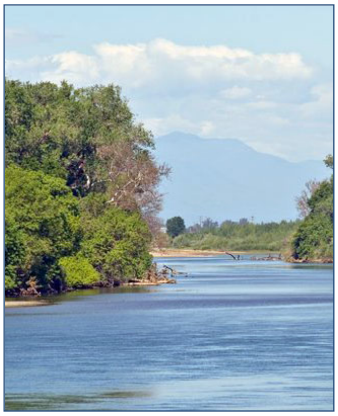
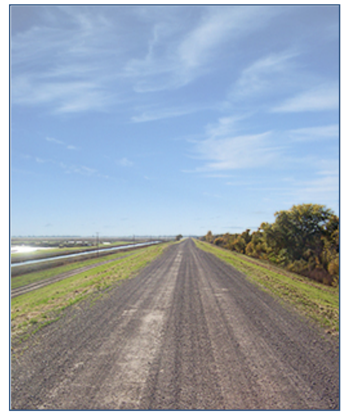
California Levee Vegetation Research Program

Burrow Dimensions of Ground Squirrels, with Special Reference to the California Ground Squirrel





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INTRODUCTION

Ground squirrels excavate subterranean burrows that provide essential protection from predators and inclement weather. Burrows may be used for refuge at night, for rearing offspring, for hibernation, or as temporary refuge from predators (Armitage 2003, Hoogland 2003, Yensen and Sherman 2003). Ground squirrels sometimes live on levees, and their burrows can threaten levee integrity by facilitating "piping" of water through the levee, by creating voids that lead to a collapse of a portion of the levee, or by promoting soil erosion that alters the levee profile (Bayoumi and Meguid 2011). Information on the length and depth of ground squirrel burrows and a knowledge of factors that influence length and depth are important for levee managers to assess the risk that ground squirrels pose to levee function. However, factors that influence the dimensions of squirrel burrows are poorly understood.

In the Sacramento Valley of California, the California ground squirrel (*Otospermophilus beecheyi*) is common on levees and is considered a threat to levee integrity because of its burrowing activities (Daar et al. 1984, Fitzgerald and Marsh 1986). Our objective was to review the literature on burrow dimensions of ground squirrels, and the California ground squirrel in particular, in order to characterize burrow dimensions of California ground squirrels and to develop an understanding of factors influencing those dimensions. Prior research indicated two factors that may influence burrow dimensions, soil characteristics and the age of the burrow. Burrows may be longer in soils that are easier to excavate but also solid enough to support the burrow (Grinnell and Dixon 1918, Alcorn 1940, Laundré and Reynolds 1993), and burrow systems occupied for a long period of time may become progressively enlarged (Fitch 1948, Reichman and Smith 1990, Smith and Gardner 1985, Armitage 2003). We investigated two additional factors, body size and degree of sociality. Home range size in mammals is positively correlated with body size (Harestad and Bunnell 1979), and the burrow system might be viewed as the below-ground portion of the home range. Hence, we expected that burrow length in particular, but perhaps burrow depth as well (Reynolds and Wakkinen 1987, Bihr and Smith 1998), would be positively correlated with body size. Social behavior varies greatly among species of ground squirrels, ranging from solitary species such as the golden-mantled ground squirrel (*Callospermophilus lateralis*) to highly social species such as the black-tailed prairie dog (*Cynomys ludovicianus*), which lives in groups composed of relatives (Armitage 1981). Because burrow systems of the more social species may be shared by multiple adults (Armitage 2003, Hoogland 2003), we expected that degree of sociality would be positively correlated with burrow length.

METHODS

We searched the literature for reports of burrow length or depth for North American species of prairie dogs (genus *Cynomys*), ground squirrels (formerly genus *Spermophilus*, but recently split into genera *Urocitellus*, *Ictidomys*, *Poliocitellus*, *Otospermophilus*, *Xerospermophilus*, and *Callospermophilus*; Helgen et al. 2009), and antelope squirrels (genus *Ammospermophilus*). We sought measures of burrows that were representative of nest burrows of adults of each species. Hence, we excluded burrows of juveniles, burrows considered to be auxiliary burrows used for temporary refuge (Armitage 2003, Yensen and Sherman 2003), and burrows likely to represent bias, such as those reported as the longest or deepest burrow encountered. We considered length to be the aggregate length of all tunnels in the burrow system. Depth was the distance below the ground surface of the nest chamber if that was reported, or otherwise the greatest depth of the burrow system. We used measures of length and depth reported by the authors, or we measured these distances from scale drawings of the burrows. For each study location for each species we calculated mean values of burrow length and depth, or used mean values reported by the authors. In two studies (Howell 1938, Turner 1973) only a range was reported, so we used the midpoint of the range as an estimate of the mean. For species-level analyses we calculated weighted averages of burrow length and depth for each study location for each species. We evaluated associations between body size and burrow length and depth, and between degree of sociality and burrow length, using correlation analysis. For body mass for each species we used the midpoint of the range given by Reid (2006). For degree of sociality for each species we used the index of social complexity for ground squirrels derived by Blumstein and Armitage (1997).

RESULTS

Burrow length and depth varied greatly among species. Burrow lengths ranged from a mean of 1.4 meters for golden-mantled ground squirrels to 26.1 meters for Utah prairie dogs (*Cynomys parvidens*) (Table 1). Burrow depths ranged from a mean of 0.2 meters for thirteen-lined ground squirrels (*Ictidomys tridecemlineatus*) to 1.8 meters for black-tailed prairie dogs and Townsend's ground squirrels (*Urocitellus townsendii*). Burrow length and depth also varied greatly within species in many cases, especially burrow length. We did not report ranges in burrow dimensions because such data were not available for some species, but examples of large ranges include burrow lengths that ranged from 2.9 to 17.4 meters for Great Basin ground squirrels (*Urocitellus mollis*) and from 3.7 to 29.3 meters for white-tailed prairie dogs (*Cynomys leucurus*).

For California ground squirrels, measures of burrow lengths ranged from 0.9 to 42.1 meters and measures of burrow depths ranged from 0.2 to 1.7 meters. The mean burrow length was 7.5 meters, but a frequency distribution of burrow lengths indicated a skewed distribution; the median burrow length was 4.6 meters, and 79% of burrows were less than 10 meters long

(Figure 1). These values agree with the characterization by Tracy Storer (Linsdale 1946) that burrows of California ground squirrels are typically 1.5 to 10.4 meters long and 0.8 to 1.2 meters deep. Burrow configuration varied as well. Some burrows consisted of a short, nearly straight tunnel, one or two entrances, and a nest chamber (Figure 2). Others consisted of a complex of tunnels extending in various directions and with multiple entrances (Figure 2).

Values of typical length and depth do not represent the maximum burrowing potential for California ground squirrels. Both the longest and the deepest burrow systems of ground squirrels ever measured were excavated by California ground squirrels. The longest burrow system was unearthed in San Luis Obispo County; it totaled 226 meters in aggregate length, had 33 entrances, displaced a total volume of 2.8 cubic meters, and was inhabited by 11 adults, 6 females and 5 males (Linsdale 1946). The deepest burrow system was unearthed in Fresno County and extended 8.5 meters below the surface (Linsdale 1946).

In comparisons among squirrel species, both burrow length ($r = 0.53$, N = 17, $P = 0.03$) and burrow depth ($r = 0.57$, N = 18, $P = 0.01$) were positively correlated with body mass (Figure 3), indicating that larger species excavated burrows that were both longer and deeper. The index of social complexity was positively correlated with burrow length ($r = 0.71$, N = 13, $P = 0.01$; Figure 4), indicating that more social species excavated longer burrow systems.

DISCUSSION

We found much variation in burrow lengths and depths, both among and within species. This variation was somewhat surprising; given the high energetic cost of excavating soil (Reichman and Smith 1990), it would seem advantageous for ground squirrels to construct burrow systems long and deep enough to satisfy basic needs, and no more than that. On the other hand, squirrels often appropriate an existing burrow left vacant by mortality, or inherit a burrow from a relative, hence the cost of excavating more extensive burrows could be spread over several generations (Reichman and Smith 1990, Armitage 2003).

Our results, along with those of prior researchers, indicate several factors that influence burrow length and depth. Soil characteristics can influence burrow dimensions, since hard soils are costlier to excavate; further, sandy soils may collapse, thereby increasing the cost of maintenance (Reichman and Smith 1990). Accordingly, both the length and depth of burrows of Wyoming ground squirrels (*Urocitellus elegans*) increased in soils characterized by a decreased bulk density and sand content and an increased percentage of silt and clay (Laundré and Reynolds 1993). Burrows of Great Basin ground squirrels (Alcorn 1940) and California ground squirrels (Grinnell and Dixon 1918) were longer in sandy than in clay soils, perhaps because sandy soils were sufficiently firm to support a burrow and clay soils were sufficiently dense to impede excavation. The presence of clay or caliche layers in sandy soil that is prone to collapse may serve as an attractant to squirrels that seem to preferentially burrow just beneath the hard layer (Alcorn 1940, Edwards 1946), potentially influencing burrow depth.

The age of the burrow system also influences burrow dimensions. Newly-excavated burrows often are shorter than established burrows (Longhurst 1944). For established burrows, periodic deposition of recently excavated earth at the burrow entrance suggests continued enlargement of the burrow system (Alcorn 1940, Fitch 1948, Armitage 2003). Smith and Gardner (1985) measured soil deposition at the burrow entrance and estimated that Columbian ground squirrels (*Urocitellus columbianus*) lengthen their burrows by an average of 4-7 meters per year.

Our results add to these findings by indicating that body size also influences burrow length and depth. The explanation for a positive relationship between burrow length and body size seems straightforward: larger squirrels require more space to carry out their underground activities. However, the explanation for the relationship between burrow depth and body size seems more obscure. Deeper burrows entail a higher energetic cost to lift excavated soil to the surface for disposal at the burrow entrance, and it is not clear why larger squirrels shoulder this cost. Burrow length and depth covary statistically ($r = 0.56$, $N = 17$, $P = 0.02$), and they may covary biologically as well. Entrance tunnels of burrow systems typically show a steep downward slope that is reduced in steepness as the burrow becomes deeper but may not become entirely level (e.g., Edge 1934, Howell 1938, Bradley 1967, Sheets et al. 1971). Hence, in some cases excavating a longer tunnel system may also mean excavating a deeper one.

Species with greater social complexity excavate longer burrow systems, a relationship that might result from either of two processes. For social species in which individuals share space underground, burrow inhabitants may excavate a larger burrow system simply to provide for the increased space needs of the multiple residents sharing the system. For species that are not highly social and normally live in individual burrows, longer burrow systems could result when expansion of neighboring burrows results in connections between burrows that are tolerated by the individual residents. These interconnected burrows may be more likely when high densities result in normally nonsocial squirrels living in close proximity.

MANAGEMENT IMPLICATIONS

Our results indicate that California ground squirrels have the potential to burrow entirely through a levee, although most burrows are much shorter than the length needed to do so. Further, burrow length is measured in terms of aggregate length of all passages in the system, and burrow systems of ground squirrels may be tortuous, include dead-end branches, and incorporate numerous entrances, all of which can contribute to length without necessarily increasing the likelihood of transecting a levee. Nonetheless, the burrow of one California ground squirrel can be long enough to perforate a levee, or shorter burrows on opposite sides of a levee can be sufficiently proximate to nearly perforate a levee, thereby increasing the risk of "piping". Further, tortuosity in burrow configuration, as well as multiple burrows in close proximity, can lead to localized voids that are prone to collapse.

Our findings, along with those of prior researchers, suggest that at least four factors influence the dimensions of burrows of California ground squirrels. One is body size—California grounds squirrels excavate burrows that are longer and deeper than some other species because they are a relatively large squirrel. Another factor is soil type. Because levees often are constructed from uncompacted material dredged from the river bottom, levees may provide favorable substrates for efficient excavation of longer burrows. When the sand content of the levee is sufficient to threaten burrow collapse, squirrels may capitalize on the presence of harder layers within the levee that can provide a "roof" for their burrow.

Time is a third factor; the longer a population of squirrels inhabits a levee, the greater the likelihood that continued excavation will result in burrow enlargement. Burrows of California ground squirrels were shorter in length in areas where squirrel numbers were regularly controlled compared with areas of little or no control (Berentsen and Salmon 2001). The fourth factor is degree of sociality, which for California ground squirrels would suggest shorter burrow lengths than for the highly social squirrels such as prairie dogs (*Cynomys* spp.). California ground squirrels are not considered highly social, and in fact they are thought to express a low degree of sociality among ground squirrels (Armitage 1981), with an index of social complexity (0.26) that is the lowest among species reported in our study. Adult females are thought to live alone and not share burrow systems with other females or with males (Boellstorff et al. 1994). Hence, it is surprising that in some cases large, complex burrow systems inhabited by multiple California ground squirrels have been excavated (Grinnell and Dixon 1918, Linsdale 1946, Ryckman 1971). However, California ground squirrels can form dense aggregations reaching 90 adults per hectare (Boellstorff et al. 1994), sometimes referred to as “colonies” (Grinnell and Dixon 1918). Perhaps interconnections among individual burrows occur when high densities persist for a period of time, interconnections that are tolerated by an otherwise nonsocial species. Such a dynamic could explain some of the large burrow systems that have been measured, including the extraordinary burrow that totaled 226 meters in length and housed 11 adult squirrels (Linsdale 1946). Hence, squirrel populations on levees that persist at high densities over time may result not only in longer burrows, but also more interconnected burrows.

ACKNOWLEDGMENTS

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Figure 1. Frequency distribution of burrow lengths (N = 25) of California ground squirrels. Three burrows longer than 12 meters (13.4, 23.8, and 42.1 meters) are not shown.

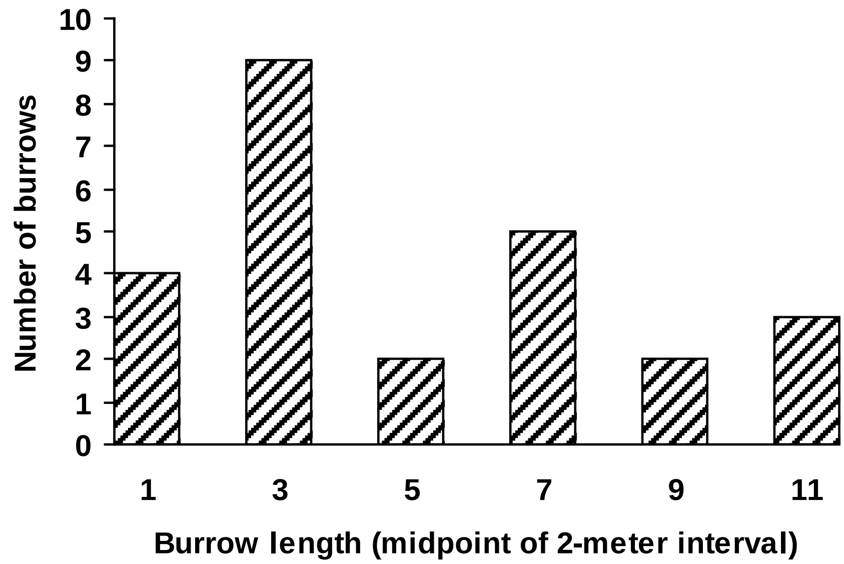


Figure 2. Diagrams of burrow systems of California ground squirrels as seen from above, illustrating a simple system with two entrances (top) and a complex system with 13 entrances (bottom). Marks at the margins are one-meter intervals. Reproduced from Ryckman (1971); numbers are locations where the author measured burrow temperature and humidity.

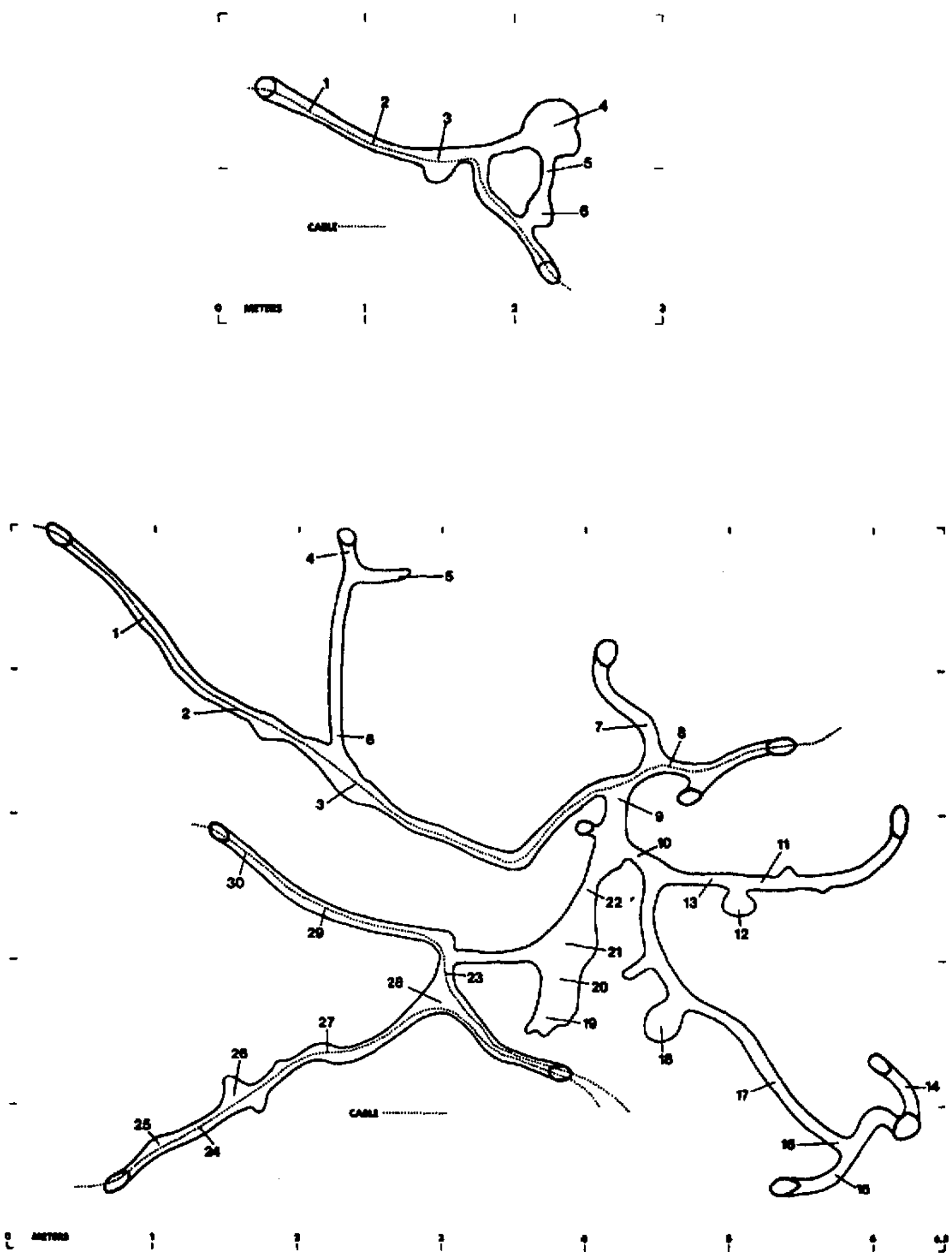
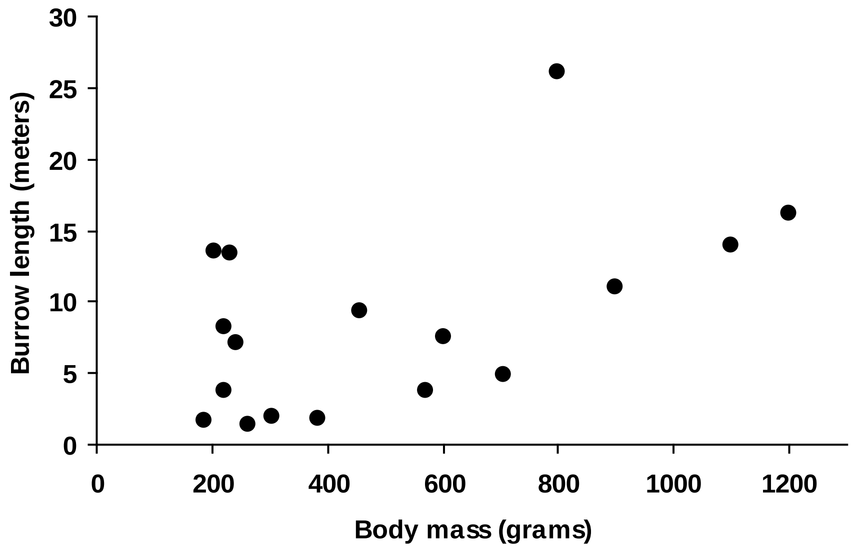


Figure 3. Relationships between body mass and mean burrow length (upper) and between body mass and mean burrow depth (lower), among species of ground squirrels.



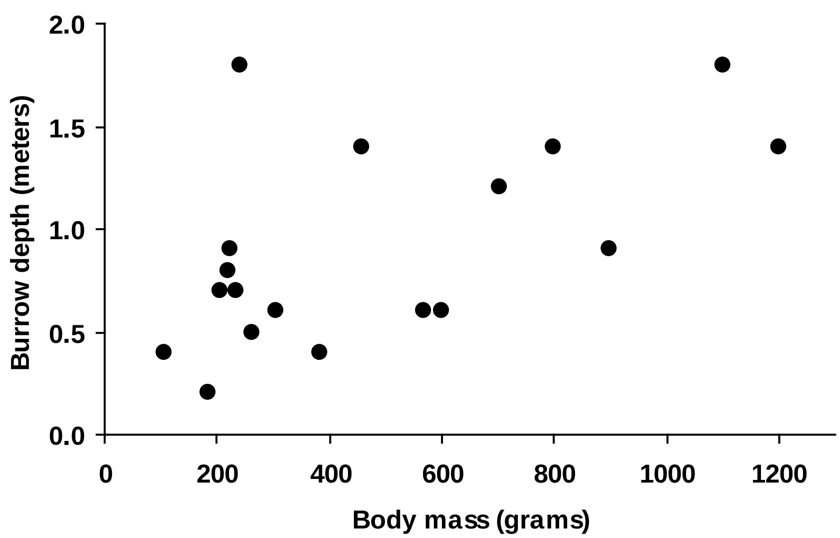


Figure 4. Relationship between degree of social complexity and mean burrow length among species of ground squirrels.

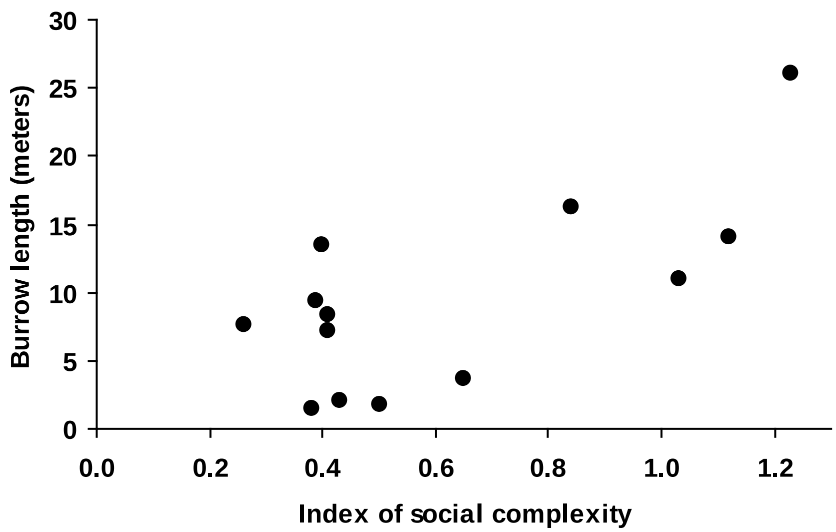


Table 1. Mean length and depth, in meters, of burrows of ground squirrels. Sample sizes are in parentheses, and reflect the total for all studies for that species.

Species	Mass (grams)	Length	Depth	References
Black-tailed prairie dog, *Cynomys ludovicianus*	1100	14.0 (30)	1.8 (29)	Whitehead 1927, Scheffer 1937, Wilcomb 1954, Sheets et al. 1971
White-tailed prairie dog, *Cynomys leucurus*	1200	16.2 (3)	1.4 (3)	Clark 1971, Burns et al. 1989, Cooke and Swiecki 1992
Utah prairie dog, *Cynomys parvidens*	800	26.1 (2)	1.4 (2)	Egoscue and Frank 1984
Gunnison's prairie dog, *Cynomys gunnisoni*	900	11.0 (13)	0.9 (13)	Foster 1924, Longhurst 1944, Smith 1982, Verdolin et al. 2008
Townsend's ground squirrel, *Urocitellus townsendii*	243	7.1 (1)	1.8 (1)	Howell 1938
Great Basin ground squirrel, *Urocitellus mollis*	222	8.3 (10)	0.9 (10)	Howell 1938, Alcorn 1940, Reynolds and Wakkinen 1987
Idaho ground squirrel, *Urocitellus brunneus*	205	13.5 (7)	0.7 (7)	Yensen et al. 1991

Table 1. Continued.

Species	Mass (grams)	Length	Depth	References
Richardson's ground squirrel *Urocitellus richardsonii*	458	9.3 (9)	1.4 (9)	Howell 1938
Wyoming ground squirrel, *Urocitellus elegans*	305	2.0 (45)	0.6 (45)	Laundré and Reynolds 1993
Belding's ground squirrel, *Urocitellus beldingi*	233	13.4 (7)	0.7 (2)	Grinnell and Dixon 1918, Turner 1973
Columbian ground squirrel, *Urocitellus columbianus*	570	3.7 (21)	0.6 (70)	Shaw 1925, Howell 1938, Young 1990
Arctic ground squirrel, *Urocitellus parryii*	705	4.9 (1)	1.2 (1)	Krog 1954
Thirteen-lined grounds squirrel, *Ictidomys tridecemlineatus*	185	1.7 (16)	0.2 (16)	Rongstad 1965, Desha 1966
Mexican ground squirrel, *Ictidomys mexicanus*	220	3.7 (2)	0.8 (2)	Edwards 1946
Franklin's ground squirrel, *Poliocitellus franklinii*	384	1.8 (5)	0.4 (5)	Haberman and Fleharty 1972
California ground squirrel, *Otospermophilus beecheyi*	600	7.5 (28)	0.6 (40)	Grinnell and Dixon 1918, Edge 1934, Ryckman 1971, Berentsen and Salmon 2001

Table 1. Continued.

Species	Mass (grams)	Length	Depth	References
Golden-mantled ground squirrel, *Callospermophilus lateralis*	263	1.4 (24)	0.5 (24)	Hatt 1927, Mullally 1953, Bihr and Smith 1998
White-tailed antelope squirrel, *Ammospermophilus leucurus*	107		0.4 (9)	Bradley 1967, Karasov 1981