MAMMALIAN SPECIES No. 382, pp. 1–5, 3 figs.

Geomys attwateri.

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Published 6 November 1991 by The American Society of Mammalogists

Geomys attwateri Merriam, 1895

Attwater's Pocket Gopher

Geomys breviceps attwateri Merriam, 1895:135. Type locality "Rockport, Texas."

Geomys breviceps ammophilus Davis, 1940:16. Type locality "Cuero, De Witt Co., Texas."

Geomys bursarius attwateri: Baker and Glass, 1951:57, name combination.

CONTEXT AND CONTENT. Order Rodentia, Family Geomyidae, Subfamily Geomyinae, *G. attwateri* is monotypic.

DIAGNOSIS. The three species of pocket gophers currently recognized in eastern Texas, *G. attwateri*, *G. breviceps*, and *G. bursarius*, are cryptic and difficult to distinguish on the basis of external characteristics. *G. attwateri* is intermediate in size between the other two species. Compared with *G. bursarius*, the dorsal exposure of the jugal bone on the dorsal surface of the zygomatic arch is shorter than the width of the rostrum in *G. attwateri* and *G. breviceps* (Schmidly, 1983).

There are distinct cytological and biochemical characteristics for these species of pocket gophers (Dowler, 1989; Tucker and Schmidly, 1981). Chromosomal races comprising the *G. bursarius* group have 2n ranging from 69 to 72, FN from 68 to 72, and an acrocentric X chromosome. Races in the *G. breviceps* group have a 2n of 74, FN of 72 or 74, and the X chromosome is submetacentric. Races in the *G. attwateri* group have a 2n of 70, FN of 72 or 74, and the X chromosome is submetacentric (Hart, 1978; Honeycutt and Schmidly, 1979). Differences in diploid number between *G. attwateri* and *G. breviceps* are best explained by a Robertsonian rearrangement, although a pericentric inversion cannot be ruled out (Dowler, 1989; Hart, 1978). *G. breviceps* is characterized by centromeric or pericentromeric C-bands, whereas *G. attwateri* contains large heterochromatic regions in the karyotypes. G-band analysis reveals that *G. breviceps* differs from *G. attwateri* by at least two centric fission-fusion events (Dowler, 1989).

GENERAL CHARACTERS. *Geomys attwateri* has a cylindrical body that is heaviest anteriorly, especially about the head (Fig. 1). There is no indication of a neck. The thickest portion of the body is at the back part of the head from which the body tapers gradually to the tail, widening across the thighs. The body is covered by short, fine hair, which is pale brown to black and usually paler ventrally. Fur-lined, external cheek pouches are used for transporting food. Eyes are small, ears are rudimentary, and tail is shortened, thickened, and naked, except for a few hairs at the base. Front feet have long, curved claws used for digging, whereas claws on the hind feet are smaller (Schmidly, 1983).

Permanent dentition consists of i 1/1, c 0/0, p 1/1, m 3/3, total 20 (Schmidly, 1983). Geomyid cranial characteristics include bisulcate upper incisors, with major sulcus near median line and minor sulcus near inner border of tooth. M3 is not strongly bicolumnar, the crown is no longer than wide owing to shortness of the posterior loph, and a shallow re-entrant fold is on the labial side. The posterior wall of P4 lacks any trace of enamel and is decidedly larger than p4 instead of subequal as in other genera. The basitemporal fossa (between coronoid process and m3) are well developed. The skull is broad with zygomata ordinarily wider across maxillary roots than across squamosal roots (Hall, 1981; Fig. 2).

Attwater's pocket gopher exhibits significant variation in body mass between ages, sexes, and among populations. Adults have greater body mass than young, 146 ± 1.3 g and 104 ± 1.8 g, respectively. Within age classes, males have greater body mass than females (adult males, 163 ± 1.6 g and adult females, 131 ± 1.2 g; young males, 106 ± 2.4 g and young females, 102 ± 2.5 g). This variation in body mass is a result of variation in growth rates. Adult growth rates are equivalent for both sexes (0.2 ± 0.2 g/month), but young males grow significantly faster than young females (8.1 ± 1.4 g/month and 2.6 ± 0.9 g/month, respectively), which accounts for observed sexual dimorphism at both ages (Williams, 1985).

Means and ranges of external measurements (in mm) for 71 *G. attwateri* from eastern Texas are (Honeycutt and Schmidly, 1979; Schmidly, 1983): total length, 216.5 (192–235); length of tail, 62.5 (51–70); length of hind foot, 26.5 (25–28). Means and ranges of skull dimensions (in mm) for these individuals are: greatest length of skull, 40.6 (37.1–44.6); length of rostrum, 16.9 (15.1–19.1); length of palatal, 23.8 (21.0–27.8); mastoidal breadth, 23.1 (21.2–25.4); palatofrontal depth, 14.3 (12.8–15.7). Means and ranges of cranial measurements (in mm) for 23 males and 33 females (in parentheses) from central Texas (Tucker and Schmidly, 1981) are: greatest length of skull, 44.6, 39.3–49.6 (41.2, 37.5–46.0); basal length, 42.4, 36.9–47.3 (38.8, 35.0–43.5); breadth of rostrum, 9.8, 8.8–11.0 (9.3, 8.4–10.1); mastoidal breadth, 24.9, 22.3–28.1 (23.4, 21.5–28.8); length of nasals, 15.3, 13.3–17.3 (13.6, 12.0–15.4); length of rostrum, 19.1, 16.0–21.5 (17.2, 15.7–19.7); zygomatic breadth, 27.7, 24.1–30.4 (25.3, 23.6–28.1); interorbital breadth, 6.4, 5.8–7.2 (6.3, 5.7–7.1); breadth of braincase, 18.8, 17.1–20.6 (17.9, 16.7–18.9); length of maxillary tooth row, 8.9, 7.6–10.1 (8.7, 7.8–9.6); palatal length, 28.9, 25.2–32.3 (26.2, 23.4–29.6); palatofrontal depth, 17.5, 16.0–18.9 (16.5, 15.3–18.2).

DISTRIBUTION. *Geomys attwateri* ranges from the Brazos River in the southcentral portion of eastern Texas (Milam and Burleson counties) south along the west bank of the Brazos River to the Gulf Coast (Matagorda County), southwest along the coast beyond Rockport (Aransas and San Patricio Counties), and northwestward to Atascosa County (Honeycutt and Schmidly, 1979; Fig. 3). Within this range, *G. attwateri* occurs in areas of suitable soil. The Brazos River is a major distributional barrier, separating *G. attwateri* from *G. breviceps* to the east. However, *G. attwateri* occupies both banks of the Colorado River in southcentral Texas. *G. personatus* is distributed to the southwest of *G. attwateri* and the ranges of these two species broadly overlap in Karnes, Goliad, Bee, and San Patricio counties (Williams, 1982).

FOSSIL RECORD. Earliest fossils of *Geomys* are known from late Hemphillian–early Blancan deposits in Kansas (Kurtén and Anderson, 1980; Russell, 1968). The Great Plains of North America is considered the center of differentiation for *Geomys* and fossils of this genus are abundant in this region throughout the Pleistocene. *Geomys* ranged west to the Pacific Ocean during the Irvingtonian (late Kansan glacial or Yarmouthian interglacial) and

FIG. 1. Attwater's pocket gopher, *Geomys attwateri*, from San Patricio County, Texas. Photograph by B. D. Eshelman.

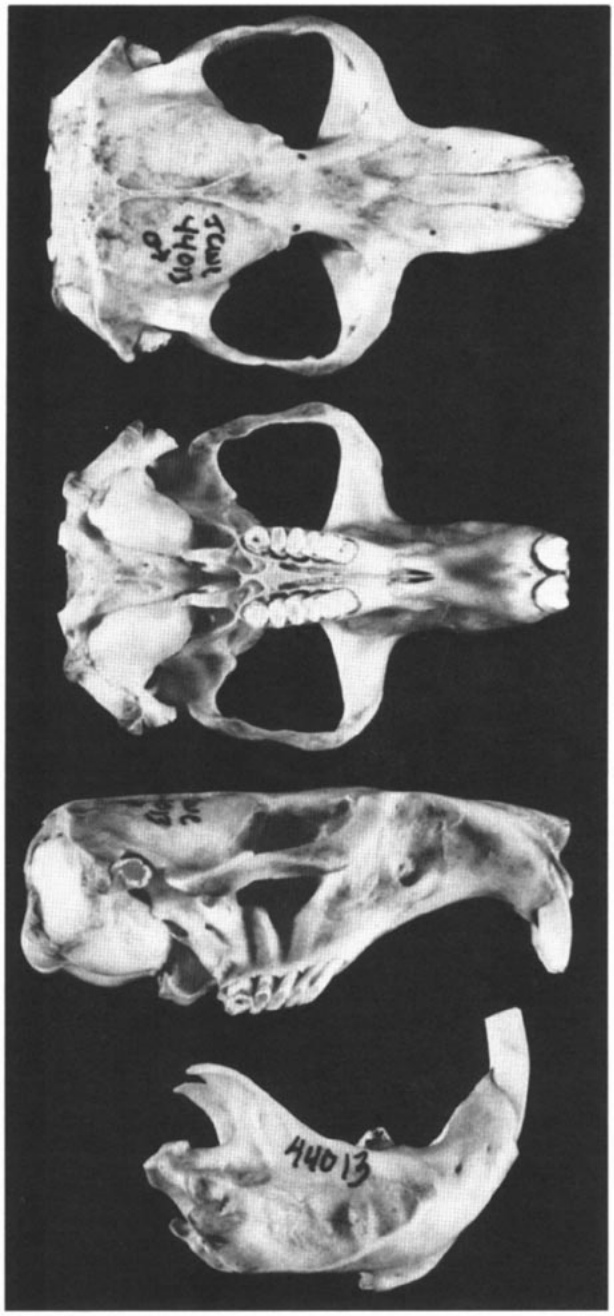

FIG. 2. Dorsal, ventral, and lateral views of skull and lateral view of lower jaw of *Geomys attwateri* from Bee County, Texas (male, Texas Cooperative Wildlife Collection, Texas A&M University, 44013). Greatest length of skull is 42.9 mm.

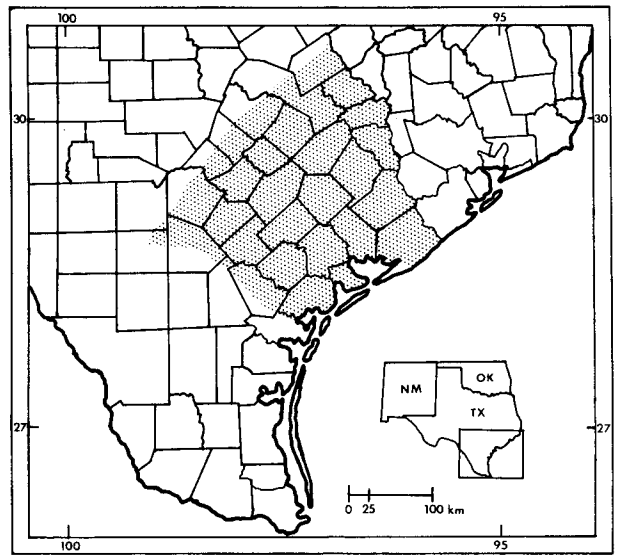

FIG. 3. Distribution of *Geomys attwateri* in southern Texas (after Honeycutt and Schmidly, 1979).

east to the Atlantic Ocean during the late Irvingtonian. *G. bursarius* is known from early Rancholabrean glacial deposits from Meade County, southwestern Kansas, and this species is widespread on the Great Plains and into central Texas by the late Rancholabrean (Lundelius, 1967; Russell, 1968). It is hypothesized that ancestors of the *breviceps* group (including *G. attwateri, G. arenarius, G. personatus,* and *G. tropicalis*) and the *bursarius* group (including *G. bursarius* and *G. lutescens*) split during the late Irvingtonian with the *breviceps* group speciating during some later time. At the close of the Pleistocene, populations of pocket gophers became restricted in the southern Great Plains as aridity increased. Relict populations of *G. breviceps* and *G. attwateri* were formed. The major features of distributions of the species of *Geomys* probably were determined by 8,000 years ago (Heaney and Timm, 1983).

FORM AND FUNCTION. The baculum of *G. attwateri* is similar in size (length = 9.86 mm, width of base = 1.70 mm) to *G. breviceps sagittalis* (length = 9.56 mm, width of base = 1.69 mm). However, the baculum of *G. attwateri* is smaller than the baculum of *G. bursarius* (length = 11.32 mm, width of base = 1.82 mm) or *G. lutescens* (length = 10.78 mm, width of base = 1.98 mm; Heaney and Timm, 1983; Kennerly, 1958*a*).

Attwater's pocket gopher has distinct summer and winter pelages, but pelage from two successive molts may be present at one time giving the appearance of continuous molt (Wilks, 1963). A spring molt (summer pelage) begins about March and ends in early July and the autumn molt (winter pelage) begins in early October, then continues until the spring molt begins. Molting begins on the head and proceeds posteriorly advancing more quickly dorsally. Two molt lines becomes apparent as a current molt ceases near the rump and a new molt begins on the head. This pattern of molting is similar to that reported for *Thomomys bottae mewa* (Howard and Childs, 1959).

Pelage of juveniles is gray (Wilks, 1963). Adult pelage usually is brownish and corresponds to soil color (Kennerly, 1959; Wilks, 1963). Subadults of either sex may have a mixture of juvenile and adult pelage. Old individuals may have grayish, grizzled fur around the eyes and nose, and inside the forelegs. White fur has been noted on heads of two individuals (Wilks, 1963).

ONTOGENY AND REPRODUCTION. No information is available on copulation and fertilization in Attwater's pocket gopher, although these activities are believed to occur belowground in all pocket gophers (Schmidly, 1983). Williams and Cameron (1990*a*) found mean ovulation rates of 2.1–3.1 eggs/female, mean embryo counts of 2.0–2.6/female, and estimated that mean size of litters ranged from 1.3–1.9/female using placental scars. Kennerly (1958*b*) reported mean size of litters was 2.5 young. In addition, Williams and Cameron (1990*a*) calculated pre-implantation mortality rates of 5–16% and post-implantation mortality rates of 17–35%. Ovulation rate varied significantly among populations, but litter size did not vary correspondingly because of differential pre-implantation and post-implantation mortality rates.

Three age classes can be differentiated (juvenile, subadult, and adult) of which only adults are sexually mature. Juveniles of either sex lack any adult pelage. Females are considered subadult when the pubic symphyses are closed and some adult pelage is present, but are considered adult when the pubic symphyses are open regardless of pelage. Subadult males have some juvenile pelage and body mass $\leq$140 g, whereas adult males generally have adult pelage and body mass >140 g (Wilks, 1963). Reproductive activity in males is determined by the presence of scrotal testes. Males with scrotal testes had visibly engorged epididymides and significantly longer testes than males without scrotal testes (17.1 $\pm$ 0.2 mm and 14.4 $\pm$ 0.4 mm, respectively; Williams, 1985). Adult females are judged reproductively active if they have open vaginas, enlarged

mammae (that is, lactating), or are obviously pregnant (Williams and Cameron, 1990*a*).

Capture of young, reproductively active individuals, and multiple captures of individuals from one burrow system have been used to determine the breeding season of Attwater's pocket gopher (Kennerly, 1958*b*; Wilks, 1963; Williams and Cameron, 1990*a*). The breeding season is from October through June (Wilks, 1963; Williams and Cameron, 1990*a*), although Kennerly (1958*b*) found that *G. attwateri* bred from November through June, except during April and May. Some reproductively active males may be found in any month (Williams and Cameron, 1990*a*). Females may have >1 litter/year (Wilks, 1963).

There is no intraspecific variation among populations of *G. attwateri* in the proportion of males and females that were reproductively active. Females in low-density populations have significantly higher ovulation rates, but not litter sizes because of higher pre-implantation and post-implantation mortality rates. These mortality effects and the lack of reproductive activity by females born into this low-density population suggest potential developmental problems for these individuals because immigrant females are reproductively active (Williams and Cameron, 1990*a*).

ECOLOGY. In a contact zone between *G. breviceps* and *G. attwateri* near College Station, Brazos County, Texas, both species occur in soils varying from sandy loam to silty clay loam in the Ships-Norwood-Yahola soil association. Neither species selected a particular soil type (Tucker and Schmidly, 1981). *G. attwateri* inhabits sandy soils (>88% sand) of the Sarita-Nueces complex on the coastal prairie of the Welder Wildlife Refuge, San Patricio County, Texas (Williams and Cameron, 1990*a*). Vegetation of the coastal prairie is dominated by perennial bunchgrasses and seasonally occurring forbs (Drawe et al., 1978). Attwater's pocket gopher also is found in habitat dominated by annual plants in southcentral Texas (Schaal and Leverich, 1982).

Stems and tubers of poppy mallow (*Callirhoe involucrata*), and stems of widow's tear (*Commelina erecta*) and bermuda grass (*Cynodon dactylon*) have been found in burrows, which suggests these plants are dietary items (Wilks, 1961, 1963). In addition, reingestion of fecal pellets by this species has been observed (Wilks, 1961). Characterization of the diet by histological analysis of stomach contents revealed the degree of dietary selection by using a statistical analysis comparing abundance of plant species in the diet to their relative availability (Williams and Cameron, 1986*a*). Perennial monocots (the most abundant dietary resource available) comprised the greatest portion of the diet and were consumed in proportion to their occurrence; perennial dicots were consumed in greater proportion than available. Reproductively active females consistently ate perennial dicots in greater proportion than available, presumably because of nutritional requirements, whereas non-reproductively active females did not. Annual dicots were consumed in significantly smaller proportions than available only when their availability was high (Williams and Cameron, 1990*a*).

Production and characteristics of pocket gopher mounds, soil nutrients, and vegetation have been compared between the site of a prescribed burn and an unburned site. Mean area of old mounds was significantly greater on the burned site, but because this site had fewer mounds, total area covered by mounds was similar for burned (9.9%) and unburned (9.4%) sites. Area and volume of newly produced mounds were similar between sites. Mean mass of soil brought to the surface/year on the sites was computed and ranged from 84,271 to 102,854 kg/ha. Soil samples collected randomly revealed that amounts of phosphorus and potassium varied between sites, but nitrate did not. Soil from mounds was significantly deficient in these three nutrients, probably as a result of leached subsurface soil present in the mounds. Analysis of biomass of vegetation clipped from randomly selected samples and from around pocket gopher mounds revealed a significant interaction between mound and burning effects. Although burning significantly decreased biomass of dicots, dicot biomass was significantly greater in samples taken around mounds on the burned site. Either mounds ameliorated the negative effect of burning on dicots, or pocket gophers concentrated their foraging in areas of higher dicot biomass, or both (Spencer et al., 1985).

Pocket gophers were removed from a 0.4-ha area and vegetation on that area was compared to one with pocket gophers present. After 30 months, species composition and richness were similar between areas, although there generally was greater frequency, cover, and biomass of vegetation on the area without pocket gophers. There was significantly less belowground biomass of perennial monocots and significantly greater aboveground biomass of perennial dicots where pocket gophers occurred. The decrease in belowground biomass may be a consumer effect and the increase in aboveground biomass may be a result of decreased competitive abilities of perennial monocots (Williams and Cameron, 1986*b*).

Artificial mounds were constructed in early spring after quantifying vegetation beneath where mounds were placed. Analyses in May showed that species diversity and biomass of dicot shoots were greater on mounds compared to randomly sampled vegetation, but these differences did not persist through October. Survival of perennials was greater than annuals on mounds, plants grew through rather than germinating on mounds, and persistence of mounds was about 7 months (Williams et al., 1986).

The impact of *G. attwateri* on vegetation of the Texas coastal prairie is significant, but short term. Such effects contribute to spatial heterogeneity of the habitat and are important because activity of pocket gophers is constant. A long-term effect of the presence of *G. attwateri* is that an annual plant community in southcentral Texas is maintained by soil disturbance (Schaal and Leverich, 1982). The effects of soil disturbance by *G. attwater* are similar to those created by military tanks, because both result in the maintenance of similar plant communities (Leverich, 1983).

Like all pocket gophers, *G. attwateri* excavates and occupies belowground burrow systems. Burrow diameters of males (8.3 ± 0.2 cm) and females (7.6 ± 0.2 cm) in southern Texas were not significantly different (Wilks, 1963). Working in the same area as Wilks, Williams and Cameron (1990*b*) found sexual dimorphism in burrow diameter of adults (7.3 ± 0.1 cm and 6.8 ± 0.1 cm for males and females, respectively), and young (6.7 ± 0.1 cm and 6.1 ± 0.1 cm for males and females, respectively). Kennerly (1958*b*) studied populations north and northwest of those studied by Wilks (1963) and Williams and Cameron (1990*b*) and reported unusually small diameters of burrows and no sexual dimorphism; means were 2.9 and 2.5 cm for males and females, respectively. Diameter of burrow is correlated with body mass (Wilks, 1963; Williams and Cameron, 1990*b*).

Mean depth of burrows does not vary with age or sex (18.4 ± 0.3 cm), but deeper burrows in spring and summer may have been in response to extension of roots of annual plants (Williams and Cameron, 1990*b*). Williams and Cameron (1990*b*) found no relationship between depth and diameter of burrows, but Wilks (1963) reported a positive correlation between these variables.

Burrow systems are complex and dynamic (Wilks, 1963). Burrow systems are more convoluted than those of other species of pocket gophers because they contain many looping tunnels, rather than a central tunnel with lateral branches. Home range (minimum area of a convex polygon containing all radiotelemetry locations for an individual) averaged 202.7 ± 72.5 m^2 and did not vary with sex (Cameron et al., 1988). Wilks (1963) reported home ranges of 307 m^2 using the same method with live-trapping data collected over 1 year (sexes pooled). Length of burrow systems does not vary with sex (90.7 ± 20.2 m), but is positively correlated with average distance moved between radio-fixes. Demographic characteristics of pocket gophers are not related to architecture of burrow systems, except for body mass of females with degree of convolution. The unique design of burrow systems may be an adaptation to low primary production or social interactions (Cameron et al., 1988).

Population density of *G. attwateri* in southern Texas ranged from 11.4 to 17.6/ha (mean, 13.6) with a peak in summer (Wilks, 1963). Sex ratio favored males (about 60%) and young comprised <24% of the population. There was significant intraspecific variation in density among seven live-trapped populations in the same study area in southern Texas with a low averaging 16.6/ha and a high averaging 43.7/ha (Williams and Cameron, 1990*a*). Temporal variation in density was similar among populations with general increases in density through the breeding season as young were recruited. The difference in densities between the two studies probably reflects the severe drought conditions during Wilks' (1963) investigation.

Equal proportions of males and females were found when age classes were pooled and for adults, but sex ratio of young was significantly biased toward males (62%). Young comprised 9.2% of seven populations. Neither sex ratio nor age structure varied among populations (Williams and Cameron, 1990*a*).

Longevity of *G. attwateri* was 6.9 months for males and 6.3 months for females (Wilks, 1963). Williams (1985) found expec-

tation of further life was equal for both sexes of adults, 12.5 ± 0.6 months. Expectation of further life for individuals captured initially as young and surviving to adult was 9.6 ± 0.9 months. Wilks' (1963) estimates were lower because his study lasted 1 year, whereas Williams (1985) conducted his study for 2.5 years.

Mortality rates of adult *G. attwateri* are equal for adult males and females, 10.2 ± 0.8%/month. Mortality of young females was similar to that of adults, 13.7 ± 4.0%/month, but mortality of young males was significantly higher, 23.7 ± 3.1%/month. In addition, mortality of young varied among populations and was negatively correlated with population density of adults (Williams and Cameron, 1990*a*).

Minimum distance between livetrap captures of Attwater's pocket gopher reveal movements from 11.3 ± 8.33 to 37.4 ± 8.56 m/day (Williams and Cameron, 1990*a*). Distance moved was negatively correlated with population density and also was greatest in an area with high availability of annual dicots (an avoided dietary resource). Cameron et al. (1988) computed a minimum-distance moved as 4.3 ± 1.4 m/h using radiotelemetry.

Low-population density of *G. attwateri* is associated with low-total recruitment, low survival of young, and longer distance moved through the habitat. Variation in dietary resources is responsible for <12% of the variation in population density and is not significantly related to other demographic variation. Perennial dicots, the food items most often selected, are significantly related to both density of adults and young. As availability of perennial dicots decreases, *G. attwateri* moves greater distances and the likelihood of aggressive encounters increases. Increased aggression results in greater loss of young through dispersal or mortality, and generally decreases recruitment (Williams and Cameron, 1990*a*). Dispersing individuals have lower body mass than residents, or were young (Williams and Cameron, 1984). In addition, dispersal by young is density dependent. Conversely, as availability of perennial dicots increases, distances moved and aggressive interactions decrease, and fewer individuals emigrate from the population. Therefore, dietary resources establish the carrying capacity and aggressive interactions provide the mechanism of population regulation (Williams and Cameron, 1990*a*).

There are numerous potential predators on *G. attwateri*, including coyote (*Canis latrans*), striped skunk (*Mephitis mephitis*), bobcat (*Lynx rufus*), western diamondback rattlesnake (*Crotalus atrox*), gopher snake (*Pituophis melanoleucus*), spotted skunk (*Spilogale gracilis*), eastern kingsnake (*Lampropeltis getulus*), prairie kingsnake (*L. calligaster*), barred owl (*Strix varia*), and barn owl (*Tyto alba*). Direct evidence of predation has been found only for coyotes (Wilks, 1963).

The distributional boundary between *G. breviceps* and *G. attwateri* roughly corresponds to the boundary between two species of lice, *Geomydoecus subgeomydis* and *G. ewingi*. *G. ewingi* generally is found on *G. breviceps* and *G. subgeomydis* usually is on *G. attwateri*. However, *G. breviceps* along the Brazos River is parasitized by *G. subgeomydis*, and *G. ewingi* is found to the west in Atascosa, Bexar, Goliad, and Wilson Counties separated from the main body of *G. ewingi* to the east by a population of *G. subgeomydis* (Timm and Price, 1980).

BEHAVIOR. Using radiotelemetry, Cameron et al. (1988) found that *G. attwateri* were equally active over a 24-h period and spent about 60% of their time at the nest site. Wilks (1963) used livetrapping to determine that peaks in activity were before noon and after sundown in summer, but there was greatest activity at night in spring and winter. He suggested that these were times of optimal temperature in burrows, but Cameron et al. (1988) found that temperatures in burrows only varied slightly and did not affect activity of pocket gophers.

Grooming is initiated as claws of the forelimbs are cleaned with the incisors, then proceeds posteriorly from the cheek pouches to the lower back. Both claws and mouth are used. Sleeping begins with the individual upright and in a curled position. Once asleep, the pocket gopher rolls over on its back, feet up, and generally has the claws of the forelimbs near or in the cheek pouches (Wilks, 1963).

Although *G. attwateri* is highly aggressive (Gregory et al., 1987), three individuals were kept together in a cage for 6 weeks without incident. Other individuals reportedly interacted by using teeth grinding, forcefully exhaling and making a wheezing sound, or presenting incisors and raising their heads (Wilks, 1963).

Pairs of Attwater's pocket gophers were released in a soil-filled arena and allowed to dig until they met. Individuals interacted in 18 of 25 pairings. Behavior, as determined by an agonistic index, did not vary among different age-sex pairings. Only five interactions resulted in physical harm to individuals, and in most trials, both pocket gophers built a soil partition between the connected burrows. No dominance was established; instead, individuals exhibited avoidance behavior (Gregory et al., 1987).

GENETICS. Three species of pocket gophers inhabit areas surrounding the range of *G. attwateri*. It is suspected that *G. bursarius* and *G. personatus* do not contact and interbreed with Attwater's pocket gopher because of microhabitat specificity (Davis, 1986; Kennerly 1959). The only known zone of contact is between *G. attwateri* (2n = 70) and *G. breviceps* (2n = 74) just west of the Brazos River in Burleson County (Tucker and Schmidly, 1981). The reason for isolation here likely is caused by meiotic imbalances and associated depression in viability from a minimum of at least two chromosomal rearrangements (Dowler, 1989). Of 42 individuals, 31% had an F1 karyotype between these two species (2n = 72, FN = 73). No karyotypically detectable backcross F2 individuals were found except in fetuses. These data indicate that F1 individuals are reproductively active and F2 hybrids are present. However, postmating-isolating mechanisms such as hybrid breakdown appear to be operating because F1 hybrids are viable, but F2 individuals do not survive. Also, nuclear DNA is not significantly different between *G. attwateri* and *G. breviceps*, but the distribution of heterochromatin and amount of chromomycin-bright heterochromatin differ markedly between these species (Burton and Bickham, 1989). Further support of isolation includes electrophoretic analyses showing that of seven polymorphic loci, five represented fixed alternate alleles between *G. attwateri* and *G. breviceps* and the genetic identity was 0.705 (Dowler, 1982). Analyses of ribosomal DNA restriction sites supports the specific distinction of *G. attwateri* and *G. breviceps* (Davis, 1986).

Two chromosomal races are present in *G. attwateri*. Race F is restricted to Milam, Burleson, and Lee counties, whereas race G is distributed from Milam County southward to the Texas coast. Electrophoretic data revealed mean heterozygosities for races F and G of 0.0 and 0.02, respectively, with a genetic identity between the races of 0.958 (Dowler, 1982). Both races have 2n = 70, but differ from each other in number of autosomal biarmed chromosomes; FN = 74 for race F and 72 for race G (Honeycutt and Schmidly, 1979). Races F and G form a contact zone in Milam and Burleson counties. Backcross and F2 hybrids could not be distinguished from F1 hybrids, but distribution of parental and hybrid Attwater's pocket gophers suggests that hybrids include backcross of F2 individuals (Dowler, 1989). C- and G-banding demonstrated that races F and G differed in one whole-arm heterochromatic change and by a paracentric inversion, but results of mitochondrial DNA analyses suggest that distinctions based on these karyotypes may be artificial (Davis, 1986).

Evolutionary relationships have been assessed employing genetic information. Hart (1978) proposed that *G. breviceps* is ancestral to the *G. bursarius* complex and that *G. attwateri* was derived from an intermediate stock with 2n = 72 and FN = 72. Assessing these relationships with karyotypes will be difficult because of large numbers of chromosomal arrangements in the genus *Geomys* (Qumsiyeh et al., 1988). Block and Zimmerman (in press) used allozymes to conclude that two major clades exist in the pocket gophers in southcentral Texas. *G. bursarius* and *G. knoxjonesi* shared a common ancestor in one clade and *G. breviceps*, *G. personatus*, and *G. attwateri* were members of the second clade with the latter two being sister taxa. Alternatively, a phylogeny based on ribosomal DNA revealed three clades, *G. breviceps*, a *G. bursarius* group (comprised of *G. bursarius*, *G. bursarius knoxjonesi*, *G. bursarius* Colorado, *G. arenarius*, and *G. lutuscens*), and a *G. attwateri* group (comprised of *G. attwateri*, *G. tropicalis*, *G. personatus*, and *G. p. streckeri*) all sharing a common ancestor (Davis, 1986).

REMARKS. The specific name *attwateri* is latinized from the last name of H. P. Attwater of San Antonio, Texas, who collected the first specimens of this species.

We thank personnel of the Texas Cooperative Wildlife Collection, Texas A&M University for loan of the skull used in Fig. 2 and for providing a list of capture localities.

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