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Geomys bursarius (Rodentia: Geomyidae)

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Abstract: *Geomys bursarius* (Shaw, 1800) is a geomyid commonly called the plains pocket gopher. A stocky rodent morphologically adapted for a fossorial life, it is 1 of 11 species in the genus *Geomys*. It occurs in southern Manitoba, Canada, and throughout the central United States southward to Texas. It prefers open grasslands and agricultural fields and is considered an economic pest. The subspecies *G. bursarius ozarkensis* is considered a species of special concern only occurring in Arkansas and *G. bursarius illinoensis* is considered a species of special concern in Indiana.

Key words: fossorial, geomyid, pest, pocket gopher, rodent

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Geomys bursarius (Shaw, 1800)
Plains Pocket Gopher

Mus bursarius Shaw, 1800:227. Type locality "upper parts of Interior Canada;" restricted to Minnesota, Sherburne Co., Elk River by Swenk (1939:6).

Mus Ludovicianus Ord, 1815:292. Nomen nudum.

Diplostoma alba Rafinesque, 1817:45. Type locality "Missouri Territory."

Diplostoma fusca Rafinesque, 1817:45. Type locality "Missouri Territory."

Geomys cinerea Rafinesque, 1817:45. Type locality "Missouri Territory."

Saccophorus bursarius: Kuhl, 1820:65. Name combination.

Mus saccatus Mitchill, 1821:249. Type locality "area bordering on Lake Superior."

Pseudostoma bursarius: Say, 1823:406. Name combination.

A[*scomys*]. *canadensis* Lichtenstein, 1825:20. Type locality "Canada;" unavailable name published in synonymy (International Commission on Zoological Nomenclature 1999: Art. 11.6).

Geomys bursarius: Richardson, 1829:203. First use of current name combination.

Geomys canadensis: LeConte, 1852:158. Name combination.

Geomys oregonensis LeConte, 1852:160. Type locality "Columbia river;" treated as obviously "erroneous" by Merriam (1895:120) because the species does not occur in Oregon.

CONTEXT AND CONTENT. Order Rodentia, family Geomyidae, subfamily Geomyinae, tribe Geomyini. *G. bursarius* is 1 of 11 species in the genus *Geomys* (Genoways et al. 2008; Patton 2005; Sudman et al. 2006). The taxonomic status of the number of *G. bursarius* subspecies has been in question, especially the *lutescens* complex. *G. lutescens* was considered a separate species from *G. bursarius* in Merriam's (1895) revision of the pocket gophers. However, subsequent work based on integration, clinal changes, and zones of contact suggested that *G. lutescens* should be relegated to *G. b. lutescens* (Burns et al. 1985; Hall 1981; Hendricksen 1972; Sudman et al. 1987; Villa-R. and Hall 1947). Yet, Russell (1968) used paleontological evidence to suggest that both were separate species, and Heaney and Timm (1983) concluded the same due to misinterpretation or by error of the evidence for integration. Further genetic analyses using mitochondrial DNA (Davis 1986), 12S ribosomal RNA (Jolley et al. 2000), and mitochondrial cytochrome-*b* gene

Fig. 1.—An adult male *Geomys bursarius* from 3 miles (4.8 km) south of Melbourne, Izard County, Arkansas. Photograph by M. B. Connior.

data (Sudman et al. 2006) support this determination. *G. b. jugossicularis* has recently been reviewed thoroughly and the most current genetic analyses elevate it to species-level recognition (Chambers et al. 2009; Genoways et al. 2008; Sudman et al. 2006). Thus, using these taxonomic decisions I recognize the following 8 subspecies of *G. bursarius*:

G. b. bursarius (Shaw, 1800:227). See above.
G. b. illinoensis Komarek and Spencer, 1931:405. Type locality "one mile South of Momence, Kankakee County, Illinois."
G. b. industrius Villa-R. and Hall, 1947:226. Type locality "1 ½ mi. N of Fowler, Meade County, Kansas."
G. b. major Davis, 1940:32. Type locality "eight mi. W of Clarendon, Donley County, Texas."
G. b. majusculus Swenk, 1939:6. Type locality "Lincoln, Lancaster County, Nebraska."
G. b. missouriensis McLaughlin, 1958:1. Type locality "2 mi. N Manchester, St. Louis County, Missouri."
G. b. ozarkensis Elrod, Zimmerman, Sudman, and Heidt, 2000:860. Type locality "3 mi. S Melbourne, Izard County, Arkansas."
G. b. wisconsinensis Jackson, 1957:33. Type locality "Lone Rock, Richland Co., Wisconsin."

NOMENCLATURAL NOTES. The generic name *Geomys* is derived from 2 Greek words, *geo* and *mys*, meaning earth rat (Rafinesque 1817). The specific epithet *bursarius* is Latin, meaning pertaining to the pouch (Schwartz and Schwartz 1981).

Literature cited within this monograph is restricted to current species boundaries of *G. bursarius*. However, literature broad in scope that does not specifically refer to the current *G. bursarius* but similar taxa, such as the closely related *G. lutescens*, may have been accidentally included in this species account.

DIAGNOSIS

Geomys bursarius is a cryptic species with other congeners and is difficult to distinguish from other species based on morphological characters. Baker and Williams (1974) provided a dichotomous key to differentiate between *G. bursarius* and other congeners. In *G. bursarius*, the dorsal exposure of the jugal is longer than the width of the rostrum, whereas in Baird's pocket gopher (*G. breviceps*), the dorsal exposure of the jugal is shorter than the width of the rostrum (Schmidly 1983). Genetic analysis is required to distinguish between *G. bursarius* and Knox Jones's pocket gopher (*G. knoxjonesi*—Bradley and Baker 1999). *G. bursarius* is larger than *G. lutescens* (Genoways et al. 2008). The karyotype of *G. bursarius* has a diploid number (2n) of 70–72 and a fundamental number (FN) of 68–74 (Hart 1978) that distinguishes it from *G. lutescens* (2n = 70–72, FN = 70–98—Hart 1978). At a contact zone in Nebraska, *G. b. majusculus* (2n = 70, FN = 68—Genoways et al. 2008) is distinct from *G. jugossicularis* (2n = 70, FN = 72—Genoways et al. 2008). In the northern portion of the range of *G. bursarius*, it can be distinguished from *Thomomys* by its grooved upper incisors (Merriam 1895).

GENERAL CHARACTERS

Geomys bursarius (Fig. 1) has a large, broad head, large front legs, well-developed claws on all legs, and a hairless, tapered tail. Females have 3 pairs of mammae: 1 pectoral, 1 abdominal, and 1 inguinal (Jones et al. 1983). Pelage varies from buff, reddish brown, liver brown, or chestnut to black (Hoffmeister 1989; Jones et al. 1985; Merriam 1895). Some individuals have a pelage containing white patches or exhibiting albinism (Hazard 1982). Cuticular scales of proximal dorsal guard hairs have an irregular petal form containing heavily crenated edges, whereas the distal portion has flattened scales (Short 1978).

Cranial features (Fig. 2) include a double presphenoid foramen, zygomata spreading, well-developed sagittal crest, frontal narrow and rounded interorbitally, and palatopterygoids broadly lingulate (Hill 1935; Merriam 1895). The nasals are not constricted near middle, squamosal arm of zygoma does not end in prominent knob over middle of jugal, and posterior end of zygomatic arm of maxilla is V-shaped at union of jugal (Hall 1981). The optic foramen in the orbitosphenoid may or may not be separated from the sphenoidal fissure by a narrow bar (Hill 1935; Merriam 1895).

Geomys bursarius exhibits sexual dimorphism, with males being larger than females. Mauk et al. (1999) found that about 50% of the variation in sexual dimorphism of *Geomys* was attributed to size and not evolutionary change in shape. In Kansas, males averaged 15.5% larger in cranial dimensions than females, ranging from alveolar length of maxillary toothrow 5.5% larger to rostral length 21.8% larger. External measurements of males were larger than those of females, ranging from length of tail 4.6% larger to body mass 84.2% larger (Hendricksen 1972).

Geomys bursarius exhibits clinal variation with respect to latitude with individuals typically being smallest in the south and largest in the north (Hall 1981). Means (mm) for standard measurements of female (n = 10) and male (n = 6) *G. bursarius* in North Dakota (Merriam 1895) were: total length, 265, 296; length of tail, 78, 90; and length of hind foot, 34, 37. Means (mm) and ranges (in parentheses) for standard measurements of samples of female (n = 3) and male (n = 5) *G. b. bursarius* from South Dakota (Jones et al. 1983) were: total length, 270 (268–272), 287 (274–295); length of tail, 68 (62–72), 77 (76–81); length of hind foot, 36 (35–37), 37 (36–39); and length of ear, 8.3 (7.8–8.5), 8.4 (8.0–9.5). Means (mm) and ranges (in parentheses) for

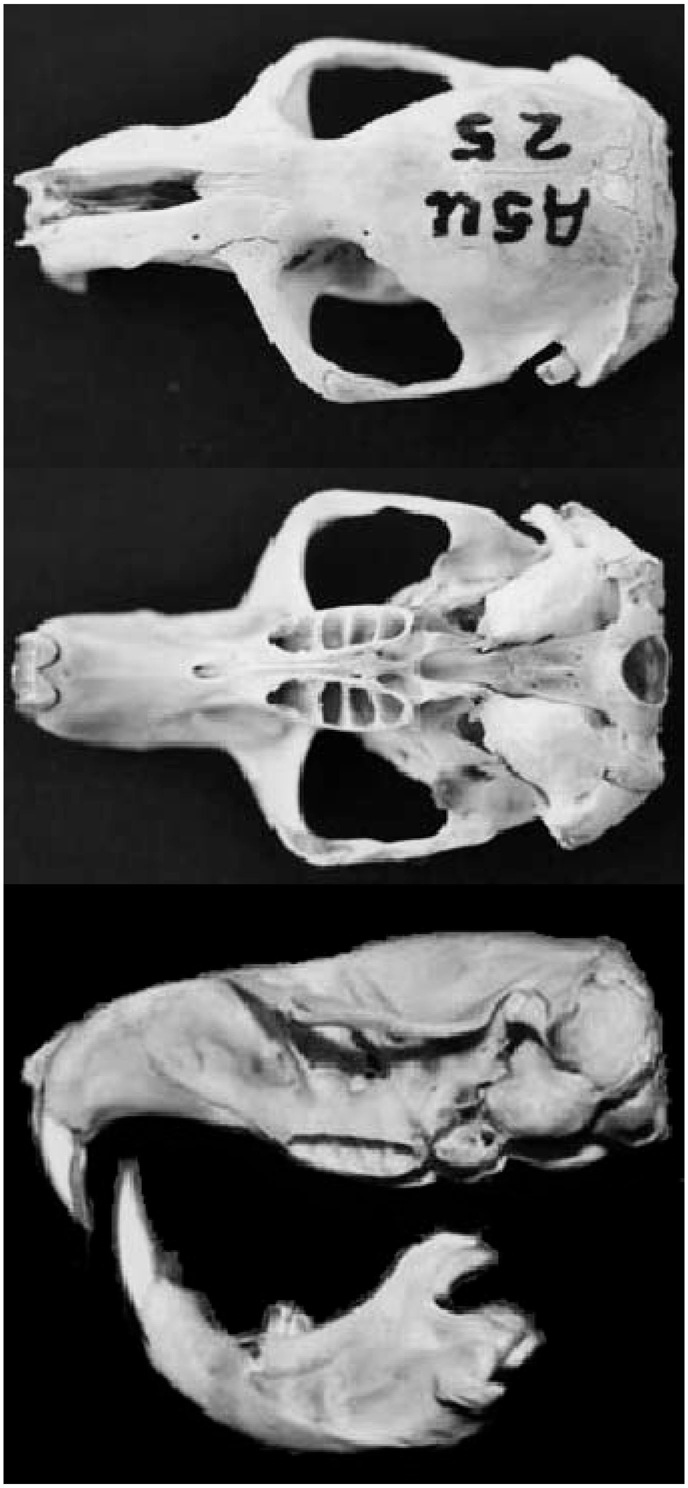

Fig. 2.—Dorsal, ventral, and lateral views of skull and lateral view of mandible of an adult male *Geomys bursarius* skull (Arkansas State University Museum of Zoology [ASUMZ] 25) from 2 miles (3.2 km) north of Melbourne, Izard County, Arkansas. Greatest length of skull is 40.9 mm.

standard measurements of female (n = 50) and male (n = 48) *G. b. majusculus* from Nebraska (Jones et al. 1983) were: total length, 290.2 (278–316), 319.6 (294–352); length of tail, 88.6 (77–102), 95.2 (75–107); length of hind foot, 35.4 (33–39), 38.7 (36–43); and length of ear, 5.6 (4–7), 6 (5–7). Means (mm) and ranges (in parentheses) for adult body dimensions of female (n = 18) and male (n = 19) *G. b. majusculus* from Kansas (Hendricksen 1972) were: total length, 263.5 (244–280), 294.9 (269–325); length of tail, 77.4 (69–88), 81 (70–97); and length of hind foot, 32 (30–35), 36.1 (34–38). Means (mm) and ranges (in parentheses) for female (n = 10) *G. b. wisconsinensis* from Wisconsin (Long 2008) were: total length, 252.2 (224–283); length of tail, 72.1 (63–90); and length of hind foot, 32.6 (31–36). Means (mm) and ranges (in parentheses [with sample size in brackets]) of the same body dimensions for female and male *G. b. illinoensis* in Indiana (Mumford and Whitaker 1982) were: total length, 258.5 (212–296 [90]), 294.3 (252–324 [48]); length of tail, 73.6 (51–100 [89]), 85.4 (67–105 [48]); and length of hind foot, 31.8 (28–37 [90]), 34.6 (35–38 [47]). Means (mm) of the same body dimensions for female (n = 20) and male (n = 4) *G. b. missouriensis* from Missouri (McLaughlin 1958) were: total length, 244.4, 278.8; length of tail, 71.7, 80.8; and length of hind foot, 29.8, 32.0. Means (mm) for external measurements for female (n = 18) *G. b. ozarkensis* from Arkansas (Elrod et al. 2000) were: total length, 208; length of tail, 53; length of hind foot, 35; and length of ear from notch, 3. Means (mm) and ranges (in parentheses) of body mass (g) of *G. b. majusculus* from Kansas (Hendricksen 1972) were 221.2 (200–247) for females (n = 3) and 407.5 (351–473) for males (n = 5); and for *G. b. illinoensis* in Indiana (Mumford and Whitaker 1982) were 231.2 (128–380) for females (n = 84) and 333.0 (230–451) for males (n = 41).

Means (mm) and ranges (in parentheses) for skull measurements for female (n = 3) and male (n = 5) adult *G. b. bursarius* from South Dakota (Jones et al. 1983) were: greatest length of skull, 49.7 (48.0–51.2) and 53.2 (51.2–54.6); and zygomatic breadth, 29.5 (28.5–30.1) and 82.6 (31.1–32.6). Those same measurements for female (n = 3) and male (n = 7) adult *G. b. majusculus* from Nebraska (Jones et al. 1983) were: 50.5 (49.4–51.8), 58.7 (56.9–61.5); and 30.4 (29.6–31.5), 36.4 (35.1–38.9). Means (mm) and ranges (in parentheses) of selected skull measurements for female (n = 20) and male (n = 20) adult *G. b. majusculus* from Kansas (Hendricksen 1972) were: condylobasal length, 46.4 (44.5–48.5), 54.3 (51.0–60.3); zygomatic breadth, 28.3 (26.9–29.8), 34.3 (31.3–38.1); mastoid breadth, 26.0 (24.6–28.0), 30.8 (28.2–35.3); squamosal breadth, 18.9 (17.9–20.3), 21.3 (18.4–25.5); palatal length, 30.2 (29.1–32.1), 36.2 (33.5–41.2); rostral length, 20.6 (19.4–23.1), 25.1 (23.0–27.8); palatal depth, 16.5 (15.4–18.1), 19.2 (17.6–21.3); rostral breadth, 10.6 (9.8–11.3), 12.3 (11.1–13.3); alveolar length of maxillary toothrow, 9.1 (8.4–10.1), 9.6 (8.9–10.5); and least interorbital constriction, 6.4 (5.8–6.8), 6.8 (6.3–7.7). Means (mm) of skull measurements for adult female (n = 11) *G. b. wisconsinensis* and adult female (n = 42) *G. b. illinoensis* (Heaney and Timm 1983) were: condylobasal length, 47.11 and 48.36; zygomatic breadth, 28.32 and 28.83; mastoid breadth, 25.84 and 27.43; and nasal breadth, 9.51 and 9.93. Means (mm) for skull measurements for adult female (n = 35) *G. b. ozarkensis* in Arkansas and adult female (n = 103) *G. b. missouriensis* in Missouri (Elrod et al. 2000) were: greatest length of skull, 42.76 and 44.91; condylobasal length, 41.50 and 43.71; basal length, 39.40 and 41.55; zygomatic breadth, 24.50 and 27.03; rostral width, 8.84 and 9.35; palatal length, 24.50 and 25.77; and mandibular length 27.79 and 29.77.

Body mass (g) of *G. b. bursarius* from Minnesota averaged 302.0 and ranged from 190.8 to 429.7 (Hazard 1982). Body mass (g) for female (n = 10) and male (n = 10) *G. b. wisconsinensis* from Wisconsin averaged (ranges in parentheses) 255.2 (224.0–283.0) and 287.6 (249.0–375.0), respectively (Long 2008). Body mass (g) for female (n = 84) and male (n = 41) *G. b. illinoensis* from Indiana averaged (ranges in parentheses) 231.2 (128.0–380.0) and 333.0 (230.0–451.0), respectively (Mumford and Whitaker 1982). Body mass (g) for female (n = 3) and male (n = 5) *G. b. majusculus* from Kansas averaged (ranges in parentheses) 221.2 (199.3–246.9) and 407.5 (351.0–473.0), respectively (Hendricksen 1972). Body mass (g) for female (n = 69) and male (n = 48) *G. b. ozarkensis* from Arkansas averaged (ranges in parentheses) 158 (130–198) and 209 (138–294), respectively (Connior 2008).

DISTRIBUTION

Geomys bursarius occurs from southern Manitoba, Canada, throughout the Midwest of the United States from Minnesota to Texas, within portions of Indiana, and west to eastern Nebraska, Kansas, Oklahoma, and New Mexico (Chambers et al. 2009; Elrod et al. 2000; Genoways et al. 2008; Hall 1981; Fig. 3). *G. b. bursarius* occurs in southern Manitoba, Canada, eastern North Dakota and South Dakota, throughout most of Minnesota, and in northwestern Wisconsin (Hall 1981). *G. b. illinoensis* occurs in northwestern Indiana between the Kankakee and Wabash rivers and east to Pulaski County and south and east of the Illinois and Kankakee rivers in Illinois (Hoffmeister 1989; Mumford and Whitaker 1982). *G. b. majusculus* occurs in eastern Nebraska and adjacent portions of southeastern South Dakota and northeastern Kansas and east through western and southern Iowa (Swenk, 1939). A narrow contact zone between *G. lutescens* and *G. b. majusculus* occurs in Antelope County, Nebraska, where *G. b. majusculus* inhabits indurate soils along the valley north of the Elkhorn River (Genoways et al. 2008; Heaney and Timm 1983). *G. b. industrius* occurs in southwestern Kansas from Meade County eastward to Pratt and Clark counties and from

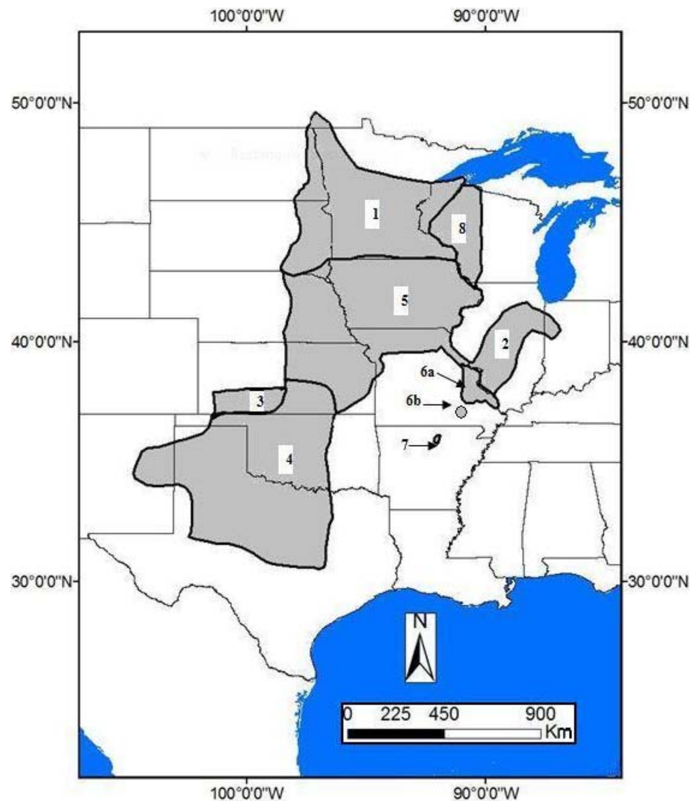

Fig. 3.—Geographic distribution of *Geomys bursarius*. Subspecies are: 1, *G. b. bursarius*; 2, *G. b. illinoensis*; 3, *G. b. industrius*; 4, *G. b. major*; 5, *G. b. majusculus*; 6a, *G. b. missouriensis*; 6b, *G. b. missouriensis* (extinct population); 7, *G. b. ozarkensis*; and 8, *G. b. wisconsinensis*. Map modified from Hall (1981), Elrod et al. (2000), Genoways et al. (2008), and Chambers et al. (2009).

Pawnee County southward to the Oklahoma border (Villa-R. and Hall 1947). *G. b. wisconsinensis* occurs throughout the western one-half of Wisconsin (Hall 1981). *G. b. major* occurs throughout the plains region of northwestern Texas, southwestern Oklahoma, and eastern New Mexico (Davis 1940). A narrow contact zone occurs in eastern New Mexico along the De Baca–Roosevelt county line between *G. b. major* and *G. knoxjonesi* (Baker et al. 1989; Pembleton and Baker 1978). On the eastern edge of the range of *G. b. major*, 2 narrow contact zones occur with *G. breviceps*. One of those zones is near Norman, Cleveland County, Oklahoma (8–10 km wide—Bohlin and Zimmerman 1982; Cothran and Zimmerman 1985; Heaney and Timm 1983), and the other occurs along the Brazos River in Falls and McClennan counties, in central Texas (Bohlin and Zimmerman 1982; Zimmerman and Gayden 1981). Further hiatus between these 2 contact zones is due to an absence of suitable soil (Bohlin and Zimmerman 1982). *G. b. missouriensis* occurs in Missouri northeast of St. Louis County (Elrod et al. 2000). Although a few individuals have been captured south of the White River (Connior et al. 2010; Elrod et al. 2000), *G. b. ozarkensis* is distributed north of the White River in the southern one-third of Izard County in north-central Arkansas (Connior et al. 2010).

FOSSIL RECORD

Fossil remains of *Geomys bursarius* have been collected in Arkansas, Colorado, Illinois, Kansas, Kentucky, Missouri, Nebraska, Oklahoma, and Texas (Kurtén and Anderson 1980). Geomyids are common in the Pliocene and Pleistocene fossil record (Russell 1968). Because species of *Geomys* are morphologically similar, the following are locations where either *G. bursarius* or morphologically similar *Geomys* have been recorded within the fossil record. *Geomys* specimens recognizable as *G. bursarius* have been found in the Pleistocene in Motley County, Texas (Dalquest 1964); Carrol Creek local fauna, Donley County, Texas (Kasper 1992); Elm Creek, Beaver County, Oklahoma (Dalquest and Baskin 1992); Duck Creek, Ellis County, Kansas (McMullen 1978); First American Bank Site, Davidson County, Tennessee (Guilday 1977); and Welsh Cave, Kentucky (Guilday et al. 1971). *G. bursarius* also has been recorded from the Wisconsinan of Illinois and Wisconsin (Hart 1978) and the middle and late Wisconsinan and early Holocene in Texas (Van Devender et al. 1987; Winkler 1990). *G. bursarius* has been recorded from the Holocene from Box Elder Creek, Caddo County, Oklahoma (Smith 1992). *Geomys* specimens collected from the late Pleistocene in Tennessee were not significantly different from modern-day *G. bursarius* and compare favorably with present populations in Illinois (Parmalee and Klippel 1981). Thus, this evidence suggests that during the late Wisconsinan, populations of *G. bursarius* occurred well south of its modern-day range in Illinois extending into Kentucky and Tennessee (Parmalee and Klippel 1981). A skull and mandible of a *G. bursarius* were found in a cave in southwestern Missouri in a rocky clay–loam deposit at a depth of about 1.5 meter believed to be possibly deposited ≥ 2,000 years before present (Brown 1995).

FORM AND FUNCTION

Form.—Dental formula is i 1/1, c 0/0, p 1/1, m 3/3, total 20. Morphological descriptions of *Geomys bursarius* include the cranial foramina (Hill 1935); middle ear (Wilkins et al. 1999); muscles of the head, neck, and pectoral appendages (Orcutt 1940); pineal gland (Sheridan and Reiter 1973); and retinal pigment epithelium and photoreceptor ultrastructure (Feldman and Phillips 1984).

Mean body size (g ± *SD*) and brain size (ml ± *SD*) for 7 *G. bursarius* were 192.4 ± 51.2 and 1.56 ± 0.18, respectively. The encephalization quotient was 0.58 and mean total dorsal surface area of those same 7 individuals was 228.6 mm^2 with the cerebrum, cerebellum, and olfactory bulbs occupying 64.875%, 27.08%, and 8.09% of that total area, respectively (Hafner and Hafner 1984).

Function.—The baculum of *Geomys bursarius* differs from that of *Thomomys* and *Cratogeomys* by the distal tip being laterally expanded and dorsoventrally flattened (Burt 1960). Basal width seems to be correlated with age (Heaney and Timm 1983). Phalli of *G. bursarius* and Attwater's pocket gopher (*G. attwateri*) are similar in regard to collar, constriction, urethral processes, midventral raphe, and epidermal structures (Williams 1982). Means (mm) and ranges (in parentheses) for standard measurements of phalli and bacula of 7 *G. b. major* (Williams 1982) were: length of distal tract, 14.1 (12.5–15.8); length of glans, 7.4 (6.5–8.3); width of glans across collar, 4.1 (3.2–4.7); width of glans across base, 3.7 (3.4–4.2); length of baculum, 10.9 (10.4–11.5); width of bacular base, 2.1 (1.5–2.8); and height of bacular base, 1.6 (1.4–2.0). The tongue of *G. bursarius* is characterized by elongated and almost entirely monofid filiform papillae with fungiform papillae being small and restricted to the anterior one-third of the tongue, but is not distinguishable from that of *Thomomys* or *Cratogeomys* (Stangl and Pfau 1994).

Geomys bursarius does not hibernate and obtains all its water requirements from its food (Downhower and Hall 1966). Pulmocutaneous water loss increases with increasing ambient temperatures. Mean resting rate of oxygen consumption of 7 individuals was 0.70 ml g^{-1} h^{-1} within the thermoneutral zone of 30–33°C (Bradley and Yousef 1975). Seasonal means of body temperature of *G. bursarius* ($n = 82$) were: spring, 35.8°C; summer, 35.4°C; autumn, 35.7°C; and winter, 35.6°C, although these differences were not significant. Basal metabolic rate was 0.946 ml O_2 g^{-1} h^{-1}, which was not significantly different from expected basal metabolic rate. Mean lethal maximum temperature for *G. bursarius* was 42.0°C with a range of 40.1–43.6°C (Montgomery 1975).

Dorsum pelage color tends to be related to moist soil color (Krupa and Geluso 2000). The loose skin and the hair arrangement permit flexibility for movement within the tunnel (Jones et al. 1983). *G. bursarius* uses the hairs around its mouth and mystacial and submental vibrissae to locate objects. *G. bursarius* uses mainly tactile cues via facial vibrissae and surrounding skin to perceive stationary objects. Furthermore, olfactory cues are used to obtain information about objects picked up in the forefeet. *G. bursarius* depends on tactile cues via lips and forelimbs more so than do nonfossorial rodents (Decoursey 1961). *G. bursarius* has a hearing range of 350 Hz to 8.7 kHz (60 dB) with a maximum sensitivity at 2 kHz and can localize sound limited to durations of 0.5 s (Heffner and Heffner 1990). *G. bursarius* exhibits the scratch digging method as opposed to the specialized chisel-tooth method of other Geomyidae, such as the giant pocket gopher (*Orthogeomys grandis*), the naked-nose pocket gopher (*Cratogeomys* [formerly *Pappogeomys*] *tylorhinus*), and the northern pocket gopher (*Thomomys talpoides*—Samuels and Van Valkenburgh

2009). *G. bursarius* has a claw length index (manus digit 3 terminal phalanx length divided by the pes digit 3 terminal phalanx length) of 2.451, which aides in the scratch digging method of breaking up soil exhibited by this species (Samuels and Van Valkenburgh 2008; Stein 2000).

ONTOGENY AND REPRODUCTION

Duration of the breeding season varies across the species' distribution. Typically, only 1 litter is produced a year, but *Geomys bursarius* may produce 2 litters during some years or in southerly locations. Pregnant females have been trapped from January to September and November in Texas (Pitts et al. 2005; Schmidly 1983), January to May in Kansas (Scheffer 1931), January to June in Missouri (Pitts and Choate 1990, 1997), March to May in Indiana (Mumford and Whitaker 1982), April to May in Minnesota (Bailey 1929), and April in Iowa and May in Wisconsin (Long 2008). Hoffmeister (1989) reported that no females ($n = 68$) collected in September, October, or November from Illinois contained fetuses. The gestation period is estimated at about 30 days but Sudman et al. (1986) reported a captive female gave birth to a single individual 51 days after isolation. Average litters based on fetus counts range in size from 2.5 (range 1–5; $n = 70$) in Texas (Pitts et al. 2005), 3.1 (range 1–5; $n = 49$) in Missouri (Pitts and Choate 1997), 4.2 (range 1–6; $n = 39$) in Kansas (Scheffer 1931), to 2.0–5.0 in Minnesota (Bailey 1929). Female hybrid crosses between *G. b. bursarius* and *G. lutescens* are able to successfully reproduce (Heaney and Timm 1985).

Subadult females develop an ossified complete pelvis; however, this pelvis reabsorbs from the symphysis region and then laterally almost to the obturator foramina. The absorption is correlated with the activities of the reproductive system and occurs during the individual's 1st proestrous and estrous period (Hisaw 1924). Reabsorption of the pubic bones is accomplished by osteoclastic activity (Hisaw 1925). Females that have bred at least once are identifiable by a reabsorbed pelvis. The corpus luteum tissue, thecal gland tissue, and the interstitial tissue are involved in the ovarian cycle (Mossman 1937). Detailed descriptions of fetal membrane development of *G. bursarius* are provided from the unfertilized tubal egg to the beginning of allantois (Mossman and Hisaw 1940) and from allantois formation to term (Mossman and Strauss 1963).

As in other *Geomys*, testes size rather than testes position is a more reliable measure of reproductive potential. Generally, in *G. bursarius*, testes $\geq$ 12.5 mm contain spermatozoa and testes $<$ 12.5 mm do not. Based on these measurements, males can potentially breed throughout the year in Texas, although the likelihood decreases in the summer and autumn (Pitts et al. 2005). Yet males are only capable of breeding from December to May based on testes size in Missouri (Pitts and Choate 1997).

Young have a body mass of about 5 g at birth and are born naked with eyes, ears, and cheek pouches closed (Fig. 4); hair becomes evident by day 10. Their eyes open at around 3 weeks and they become weaned at around 4–5 weeks (Sudman et al. 1986). Juveniles are able to freely move about within the natal burrows and start to construct individual burrows at around 40 g of body mass (Connior and Risch 2009a). An individual juvenile female *G. b. ozarkensis* in Arkansas increased in mass from 44 g to 61 g in 36 days (Connior and Risch 2009b). In captivity, adult mass and total length were reached around day 100 (Sudman et al. 1986). Juvenile pocket gophers probably combine both burrow extension from natal burrow and aboveground dispersal to establish new territories after being displaced from their natal burrow after weaning.

ECOLOGY

Population characteristics.—Densities of *Geomys bursarius* are highly variable and are probably related to the size of area sampled and quality of habitat. In Texas, densities ranged from 1.3, 16.0, and 18.7 individuals/ha in pastureland, riparian sandbar, and hayfield, respectively (Broussard 1996). Average density estimates per hectare were 20.4 (range 4.0–60.4) in Arkansas (Connior et al. 2010), 7.4–9.9 in Indiana (Mohr and Mohr 1936), 12.9 in Wisconsin (Zinnel 1992), and 5.4–22.0 in Minnesota (Adams 1966). Smallwood and Morrison (1999) determined that generally much of the variation can be explained by the size of the study area.

Limited studies on survival estimates and environmental mortality factors have been conducted in *G. bursarius*. In a radiotelemetry study in Arkansas, higher mortality occurred in the winter and spring season than in the summer (Connior and Risch 2010). In Minnesota, Adams (1966) estimated a

Fig. 4.—A neonate *Geomys bursarius* from 3 miles (4.8 km) south of Melbourne, Izard County, Arkansas (Arkansas State University Museum of Zoology [ASUMZ] 28492). Photograph by M. B. Connior.

turnover rate of 4.5 years. Yet the maximum age of *G. bursarius* may exceed 7 years in the wild (Downhower and Hall 1966). Predators and direct killing from humans are a common source of mortality. Mortality of *G. bursarius* has been documented as a direct result of the use of heavy farm equipment within fields (Connior and Risch 2010). Environmental factors contributing to mortality include flooding (Connior and Risch 2010) and a combination of rain and cold temperatures leading to death (Bailey 1895).

Populations tend to be female biased with 64% of trapped individuals being female in Arkansas (Connior 2008), 62% and 66% in Indiana during 2 separate studies (Conaway 1947; Tuszynski 1971), 62% in Missouri (Pitts and Choate 1997), 60% in Texas (Pitts et al. 2005), and 65% in Minnesota (Adams 1966). During a collection for the Illinois Museum of Natural History, 61% of 121 pocket gophers collected during October–December were females (Hoffmeister 1989). In the collection at University of Wisconsin–Steven's Point, 60% are female (Long 2008).

Space use.—*Geomys bursarius* inhabits a broad range of habitat types including tallgrass prairie (Benedix 1993; Davis et al. 1997; Finck et al. 1986; Klaas et al. 1998), nonnative grassland (Behrend and Tester 1988; Broussard 1996; Connior et al. 2010; Downhower and Hall 1966; Pitts and Choate 1997; Reichman and Smith 1985), cultivated land (Behrend and Tester 1988; Downhower and Hall 1966; Pitts and Choate 1997), and urban areas (Pitts and Choate 1997). *G. bursarius* seems to be restricted to habitat based on sand and loam content of soil more so than by herbaceous structure in the habitat. In Kansas, *G. bursarius* prefers soils with a minimum sand content of 40% and a maximum clay and silt content each of 30% (Downhower and Hall 1966). Furthermore, *G. bursarius* prefer high sand and low clay contents in Texas (Schmidly 1983) and Arkansas (Connior et al. 2010). Soil pH does not seem to limit the distribution of *G. bursarius* (Connior et al. 2010).

Three burrows in northwestern Oklahoma averaged 139 m^2 in area (Watts 1970). Home ranges (*SE*) of *G. bursarius* in Kansas averaged 34.5 ± 10.2 m^2 (n = 38), whereas in Minnesota home ranges averaged 95.3 ± 28.6 m^2 (n = 20) when estimated by excavation of burrow (Romañach et al. 2005). Home ranges in Minnesota averaged 66.3 ± 23.2 m^2 (n = 16) when estimated by radiotelemetry data points (Artmann 1967). In another study in Minnesota, male home ranges averaged 150 m^2 and female home ranges averaged 206.7 m^2 when estimated by radiotelemetry (Zinnel 1992). In Arkansas, adult females had an average home-range size of 287.1 ± 196.8 m^2 (range 67.9–823.2 m^2; n = 21) and adult males had an average of 291.8 ± 162.2 m^2 (range 23.7–546.5 m^2; n = 14) with no difference between sexes. Subadult females had an average home-range size of 225.2 ± 151.8 m^2 (range 47.9–439.8 m^2; n = 12) and subadult males had an average home-range size of 246.2 ± 70.9 m^2 (range 34.3–533.7 m^2; n = 7). Home-range size was directly related to body mass for subadult females, yet indirectly related for adult females. Home-range size was not related to body mass for either subadult or adult males (Connior and Risch 2010).

Burrows of *G. bursarius* had an average total length, depth, and diameter of 30.7 m, 23.7 cm, and 7.7 cm, respectively, in Texas (n = 10; mean mass 148 g—Wilkins and Roberts 2007); 115.7 m, 5.1 cm, and 7.4 cm, respectively, in Oklahoma (n = 3—Watts 1970); and 76.1 m, 21.1 cm, and 8.0 cm, respectively, in Kansas (n = 5—Downhower and Hall 1966; Scheffer 1940; Smith 1948). Nests are constructed underground and consist of grass and other herbaceous material (Fig. 5). Underground nests (n = 4) in Kansas were an average of 50.2 cm below ground and 2 had diameters of 17.8 and 15.2 cm, whereas the other 2 had dimensions of 10.6 by 15.2 cm and 17.8 by 8.9 by 16.5 cm (Downhower and Hall 1966; Scheffer 1940; Smith 1948). In Arkansas, 7 nests were on average 47 ± 12 cm below the soil surface (range *SD* 30–70 cm) and had the following dimensions: height 21 ± 4 cm (range 15–25 cm), width 22 ± 4 cm (range 13–27 cm), and length 23 ± 5 cm (range 18–30 cm—Connior 2008).

Areas containing *G. bursarius* are easily recognized by the surface mounds produced during foraging and tunnel excavation (Fig. 6). *G. bursarius* impacts soil distribution and nutrients, indirectly affecting plant distribution and composition. Tunnel excavation rate is directly related to body mass in plots with the highest belowground plant biomass (Andersen 1987). *G. bursarius* excavated ≥ 112 m of tunnel during 158 days and deposited the soil in 134 surface mounds, 68 plugs, and 77 m of backfilled tunnels while in captivity (Thorne and Andersen 1990). Volume of mounds deposited by *G. bursarius* in Indiana ranged from 1 to 108 l with a mean *SE* of 13.7 ± 0.61 l (n = 376) and mound area averaged 0.25 ± 0.007 m^2 (range 0.03–1.13 m^2—Sparks and Andersen 1988). Surface area of mounds of *G. bursarius* in Minnesota averaged 0.18 m^2 with an average of 1,220

Fig. 5.—Nest of adult male *Geomys bursarius* located ca. 50 cm below ground from Izard County, Arkansas. Note the nest is composed of grassy material. Photograph by M. B. Connior.

Fig. 6.—Surface dirt mounds produced by *Geomys bursarius* while foraging and constructing tunnels in Izard County, Arkansas. Photograph by M. B. Connior.

mounds ha^{-1} $year^{-1}$, which is comparable to 2.2% of the soil surface per year (Tilman 1983). Two fields in Minnesota had densities of 230 and 212 mounds/acre or 37 and 39 mounds/gopher, respectively (Adams 1966). Gophers constructed a mean rate of 660–1,280 cm/day of tunnels in enclosures containing carrots (Andersen 1987), whereas they constructed $\leq$ 290 cm/day in enclosures without carrots (Thorne and Andersen 1990). This amount of soil redistribution greatly affects the distribution of nutrients. In fact, *G. bursarius* increased the potassium cation in newly formed mounds and increased nitrogen in the 21- to 30-cm soil zone but decreased nitrogen in the 1- to 10-cm soil zone in Minnesota (Grant and McBrayer 1981; Zinnel and Tester 1992). The disturbances of *G. bursarius* reduce shallow soil nitrogen ultimately slowing succession (Inouye et al. 1987a, 1987b).

Geomys bursarius produced significantly more mounds on nitrogen-fertilized plots than on unfertilized plots, resulting in increased soil height (Inouye et al. 1997). In Iowa, mound production was greatest in summer thereby contributing to patches of bare ground during the growing season (Klaas et al. 2000). In Minnesota, *G. bursarius* buried 2.2% of *Penstemon grandiflorus* by mound production, yet *P. grandiflorus* never occupied an opening that was not inhabited by *G. bursarius* (Davis et al. 1991, 1997). Graminoids were in higher proportions in annually burned and unburned prairie containing mounds of *G. bursarius* than in undisturbed prairie (Gibson 1989). Total-plant and graminoid species richness along with mean graminoid, forb, and total-plant biomass was significantly lower on areas with newly created mounds than adjacent to mounds or in undisturbed tallgrass-prairie communities, but no difference was detected 2 years after disturbance (Rogers et al. 2001). Yet vegetation biomass was lowest in areas with high activity of *G. bursarius* versus areas lacking pocket gopher activity in Minnesota (Reichman and Smith 1985). Annual tree mortality due to activity of *G. bursarius* averaged 1.85% in Minnesota, representing a significant source of mortality (Inouye et al. 1994). Root biomass at den sites of *G. bursarius* versus control sites was not different in the 1- to 10-cm zone, but was significantly different at both the 11- to 20-cm and 21- to 30-cm zones in Minnesota (Zinnel 1992).

Diet.—*Geomys bursarius* primarily feeds on the roots and stems of forbs and grasses, making it a specialist herbivore because these are the particularly fibrous portions of the plant (Samuels 2009). Bailey (1895) reported that the stomach contents of 7 gophers collected from Minnesota and South Dakota contained 100% vegetation matter consisting mainly of roots. In Minnesota, stomach and fecal samples of free-ranging gophers contained 94% grasses and 6% forbs with *Bromus*, *Agropyron*, *Avena*, and *Poa* being the most prevalent grasses and *Erigeron* and an unidentifiable Brassicacae being the most common forbs (Behrend and Tester 1988). In Illinois, *G. bursarius* is known to feed on the roots, stems, and leaves of sweet clover, alfalfa, bluegrass, and dandelion (Hoffmeister 1989). An individual trapped in Indiana had wheat (*Triticum*) plants in its cheek pouches (Mumford and Whitaker 1982). Captive animals from Indiana consumed human foods including oranges, tomatoes, and watermelon (Conaway 1947).

Geomys bursarius caches food within chambers inside the burrows. One burrow in eastern Kansas contained 2 food caches composed entirely of tubers of sunflower (*Helianthus tuberosa*) weighing 238.0 g with 39 pieces and 444.5 g with 90 pieces (Smith 1948) and another burrow contained a food cache entirely of Johnson grass (*Sorghum halpense*—Downhower and Hall 1966). Conaway (1947) found 2 food caches that consisted almost entirely of roots of alfalfa. Fresh scats of *G. bursarius* are dark brown, oblong, contain vegetable matter, and measure on average 11 by 4 mm, whereas dehydrated scats are darker in color and average 8 by 3.5 mm (Conaway 1947).

Diseases and parasites.—Although limited studies have been conducted, *Geomys bursarius* does not commonly exhibit any diseases or morphological health conditions. During a statewide survey of Oklahoma for rodent-borne viral diseases, *G. bursarius* (n = 2) did not harbor antibodies against any of the tested viral diseases (Nisbett et al. 2001). Although arthritis is prevalent among medium and large-sized wild mammals, none of the mature small mammals, including a single *G. bursarius*, tested showed any evidence of arthritis (Greer et al. 1977).

Endoparasites of *G. bursarius* include the nematodes *Capillaria americana*, *C. hepatica*, *Litomosa filaria*, *Mastophorus muris*, *Physaloptera limbata*, and *Ransomus rodentorum*; and the cestodes *Andrya macrocephala*, *A. translucida*, *Anoplocephaloides infrequens*, *A. variabilis*, *Cittotaenia perplexa*, *Hymenolepis diminuta*, *H. weldensis*, *Monoecocestus anoplocephalaloides*, and *Oochoristica* (Bartel and

Gardner 2000; Burnham 1953; Douthitt 1915). The acanthocephalan *Moniliformis clarki* has been recorded from *G. b. bursarius* in Minnesota (Bartel and Gardner 2000), *G. b. illinoensis* in Illinois (Van Cleave 1953), and *G. b. missouriensis* in Missouri (Amin and Pitts 1996). Cestodes believed to be in the genus *Hymenolepis* were collected from *G. bursarius* from South Dakota (Keitzmann 1987). Rissky (1962) reported that 98% of *G. bursarius* collected from Clay County, South Dakota, harbored larval cestodes in the mesenteries of the lungs, liver, heart, and diaphragm and cecal smears from 28% of them harbored the small flagellated protozoan *Monocercomonoides*. Upton et al. (1992) reported the coccidia *Eimeria geomydis* from *G. b. missouriensis* and *G. b. illinoensis*.

Ectoparasites of *Geomys bursarius* include the fleas (Siphonaptera) *Ctenophthalmus pseudagyrtes* and *Opisocrostis bruneri*; the chewing lice (Mallophaga) *Geomydoecus geomydis*, *G. illinoensis*, *G. spickai*, and *G. oklahomensis*; the tick (Acari) *Dermacentor variabilis*; and a hypopi of *Dermacarus hypudaei* (Bartel and Gardner 2000; Coffman 1972; Elrod et al. 1996; Spicka 1981; Timm and Price 1980; Tuszynski and Whitaker 1972; Wilkins and Houck 2001). The host–parasite relationship of pocket gophers and chewing lice has been well studied and the following relationships exists: *Geomydoecus geomydis* parasitizes *G. b. bursarius*, *G. b. majusculus*, and *G. b. wisconsinensis*; *Geomydoecus illinoensis* parasitizes *G. b. illinoensis*; *Geomydoecus oklahomensis* parasitizes *G. b. industrius* and *G. b. major*; and *Geomydoecus spickai* parasitizes *G. b. missouriensis* and *G. b. ozarkensis* (Elrod et al. 1996; Timm and Price 1980). Mites (Acarini) that parasitize *G. bursarius* include *Androlaelaps geomys*, *Echinonyssus geomydis*, *E. longichelae*, *Euschongastia trigenuala*, *Geomylichus floridanus*, *G. geomydis*, *Haemogamascus reidi*, and *Pseudoschoengastia farneri*. Nonparasitic mites that have been found on *G. bursarius* include the family Anoetidae, *Cyrtolaelaps*, *Dendrolaelaps*, *Imperipes* (*I.*) *spickai*, *Macrocheles spickai*, *Oribella*, *Parasitus*, *Pergamasus*, *Pygmephorus designates*, *P. plurispinosus*, *P. rackae*, *P. spickai*, *P. scalopi*, *P. whitakeri*, the family Saproglyphidae, *Scutacarus geomyi*, and *S. missouriensis* (Coffman and McDaniel 1975; Downhower and Hall 1966; Krantz and Whitaker 1988; Smiley and Whitaker 1979; Spicka 1981; Tuszynski and Whitaker 1972; Ubelaker and Downhower 1965; Wilkins and Houck 2001).

Interspecific interactions.—Numerous insects occupy burrows of *Geomys bursarius*, including camel crickets; rove, histerid, and scarab beetles; and anthomyiid flies. In Arkansas, insects collected in burrows of *G. bursarius* include the cave crickets *Ceuthophilus fusiformis* and *Ceuthophilus* (undescribed species); anthomyiid flies; rove beetles; the hister beetles *Atholus minutes*, *A. nubilus*, *Geomysaprinus* (undescribed species), *Onthophilus kirni*, and *Spilodiscus gloveri*; and the scarab beetles *Cryptoscatomaster haldemani*, *C. oklahomensis*, *Dellacasiellus kirni*, *Geomyphilus insolitus*, and *Scabrostomus sepultus* (Kovarik et al. 2008). In Wisconsin, 6 species of scarabaeidae (*Cryptoscatomaster iowensis*, *C. magnificens*, *C. punctissimus*, *Dellacasiellus kirni*, *Geomyphilus insolitus*, and *Scabrostomus peculiosus*) were found in the burrows (Kriska and Katovich 2005). Additionally, *Anomala binotata*, *Cremastocheilus castaneus*, *C. knochi*, and *Euphoria inda* have been collected from the mounds of *G. bursarius* (Kriska and Young 2002). The scarab beetles *Dellacasiellus concavus*, *Geomyphilus thomomysi*, and *G. russeus* also have been recorded in the burrows of *G. bursarius* (Gordon and Skelley 2007). In addition, 2 species of carrion beetles (Leiodidae), *Sciodrepoides watsoni hornianus* and *Catops geomysi*, are known to occupy burrows of *G. bursarius* (Peck and Skelley 2001).

Reptiles and amphibians documented using burrows and mounds of *G. bursarius* include Hurter's spadefoot (*Scaphiopus holbrookii hurterii*), three-toed box turtle (*Terrapene carolina triunguis*), common map turtle (*Graptemys geographica*), rough earth snake (*Virginia striatula*), eastern racer (*Coluber constrictor*), eastern coachwhip (*Masticophis flagellum*), and bullsnake (*Pituophis catenifer*—Connior et al. 2008; Scheffer 1931). Tiger salamanders (*Ambystoma tigrinum*) have been recorded from other *Geomys* burrows and probably occur within the burrows of *G. bursarius* as well. Mammals that use burrows of *G. bursarius* include eastern spotted skunk (*Spilogale putorius*), long-tailed weasel (*Mustela frenata*), and least weasel (*M. nivalis rixosa*—Florine 1942; Polder 1968; Scheffer 1931). Klaas et al. (1998) found that meadow vole (*Microtus pennsylvanicus*) activity was inversely related to activity of *G. bursarius*. These results suggested that increased mound production set maximum levels on activity of *M. pennsylvanicus* but not minimum levels. Connior et al. (2008) documented 45 species of reptiles and amphibians and small mammals occupying habitat of *G. b. ozarkensis*, many of which potentially use burrows excavated by pocket gophers. *G. bursarius* also is a common associate of black-tailed prairie dogs (*Cynomys ludovicianus*) in Oklahoma (Tyler and Shackford 2002).

Predators of *G. bursarius* include several snake species: *Crotalus atrox* (Beavers 1976; Pisani and Stephenson 1991), *C. horridus* (Ernst and Ernst 2003), *Lampropeltis calligaster calligaster* (Connior et al. 2009), and *Pituophis catenifer* (Scheffer 1931). Mammalian predators of *G. bursarius* include feral cat (*Felis catus*), coyote (*Canis latrans*), *Mustela frenata*, *Spilogale putorius*, American badger (*Taxidea taxus*), gray fox (*Urocyon cinereoargenteus*), and red fox (*Vulpes vulpes*—Best et al. 1981; Hatfield 1939; Lampe 1982; Polderboer et al. 1941; Scheffer 1931; Scott 1955; Zinnel 1992). *G. bursarius* has been recorded in the prey of barn owl (*Tyto alba*—Goyer et al. 1981; Scheffer 1931), burrowing owl (*Athene cunicularia*—McCracken et al. 1985; Tyler 1983), long-eared owl (*Asio otus*—Cahn and Kemp 1930; Scheffer 1931), great horned owl (*Bubo virginianus*—Scheffer 1931), red-tailed hawk (*Buteo jamaicensis*—Hegdel and Gatz 1976), ferruginous hawk (*Buteo regalis*—Cartron et al.

2004), bald eagle (*Haliaeetus leucocephalus*—Boal et al. 2006), and great blue heron (*Ardea herodias*—Peifer 1979).

BEHAVIOR

Geomys bursarius is territorial, spending most of its time below ground in solitary burrows, and exhibits agnostic behavior while in the presence of conspecifics. It will commonly investigate nearby vacant burrows, but rarely investigates occupied burrows. Larger *G. bursarius* displaced smaller ones 71% of the time during combat (Zinnel and Tester 1994). *G. bursarius* will come above ground to forage and disperse (Andersen 1987; Connior and Risch 2010).

Geomys bursarius exhibits a bimodal pattern of activity, most likely to be active at night (2200–0600 h) and early afternoon (1300–1700 h) possibly to avoid burrow temperature extremes. *G. bursarius* was active away from its nests for an average of 400 min/day with morning bouts the shortest, afternoon bouts the longest, and for intermediate lengths during the night (Benedix 1994). Adult females observed via radiotelemetry relocated $> 50\%$ after raising a litter, leaving female offspring in possession of the natal den site (Zinnel and Tester 1994). In captivity, *G. bursarius* sometimes will eat its offspring (Johnson 1926; Sudman et al. 1987).

Adult male ($n = 5$) and adult female ($n = 9$) *G. bursarius* were able to swim on average 361 and 236 s, respectively while in water shallow enough to allow them to occasionally touch bottom. A juvenile male was able to swim for 885 s (Best and Hart 1976).

Geomys bursarius exhibits an optimal foraging strategy known as an area-restricted search. They accomplish this by concentrating their foraging tunnels around areas of abundant and storable food sources, thus minimizing energy expenditures during foraging (Andersen 1988; Benedix 1993; Watts 1970). Cellulolytic bacteria in the digestive tract of *G. bursarius* help to maximize digestion, aiding in its energy budget (Boley and Kennerly 1969).

GENETICS

Diploid chromosome numbers (2n) for *Geomys bursarius* range from 70 to 72, with the range of fundamental number (FN) being from 68 to 74 (Hart 1978). *G. b. major* exhibits a diploid number of 70, 71, and 72 (Baker et al. 1983, 1989; Patton et al. 1980) with a large acrocentric X chromosome and a small acrocentric Y chromosome (Honeycutt and Schmidly 1979). *G. b. industrius* is chromosomally distinct with a large biarmed X chromosome (Hart 1978). Average genetic distance based on the Kimura-2 parameter model of evolution within *G. bursarius* is 3.78 for mitochondrial gene data (Sudman et al. 2006).

Hybridization occurs between *G. b. majusculus* and *G. lutescens*, *G. b. major* and *G. knoxjonesi*, and *G. b. major* and *G. breviceps* (Baker et al. 1989; Bohlin and Zimmerman 1982; Cothran and Zimmerman 1985; Genoways et al. 2008). A historical hybrid zone occurs in Runnels County, Texas, between *G. b. major* and *G. knoxjonesi*, possibly during the end of the Pleistocene or early Holocene (Jones et al. 1995). At the New Mexico contact zone between *G. b. major* and *G. knoxjonesi*, most of the hybrid crosses were between females of *G. knoxjonesi* and males of *G. b. major* (Baker et al. 1989). Bradley et al. (1991) reported that these individuals exhibited unidirectional mating of females of *G. knoxjonesi* and males of *G. b. major*. At the Oakdale hybrid zone between *G. b. majusculus* and *G. lutescens* in Nebraska, 27 of 30 hybrid crosses involved females of *G. b. majusculus* and males of *G. lutescens* (Genoways et al. 2008).

CONSERVATION

The subspecies *Geomys bursarius ozarkensis* is considered a "species of greatest conservation need" with an S1 ranking (Critically Imperiled) in Arkansas because of its restricted distribution and separation from other subspecies (Anderson 2007) along with its small population size (Kershen 2004). The subspecies *G. b. illinoensis* is considered a species of "Special Concern" in need of further study in Indiana (Case and Associates 2006). Although pocket gophers, including *Geomys*, are considered economic pests because of their burrowing and foraging behaviors (Witmer and Engeman 2007), *G. bursarius* provides additional habitat from these burrowing and foraging behaviors that is utilized by many other organisms.

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ALFRED L. GARDNER reviewed the synonymy. Editor was MEREDITH J. HAMILTON.