Microtus miurus (Rodentia: Cricetidae)

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Abstract: *Microtus miurus* Osgood, 1901, is a cricetid commonly called the singing vole. An average-sized, short-tailed vole, it is 1 of 62 species in the genus *Microtus*. It occurs in northwestern Canada and Alaska, where it inhabits well-drained tundra and extends into subalpine and alpine regions. It is unique among arvicolines in that it not only hoards underground but also constructs haypiles above ground. It is listed as a species of "Least Concern" by the International Union for Conservation of Nature and Natural Resources. DOI: 10.1644/855.1.

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Microtus miurus Osgood, 1901
Singing Vole

Microtus miurus Osgood, 1901:64. Type locality "head of Bear Creek in mountains near Hope City, Turnagain Arm, Cook Inlet, Alaska."

Microtus miurus oreas Osgood, 1907:61. Type locality "Toklat River, Alaskan Range, Alaska."

Microtus muriei Nelson, 1931:311. Type locality "Kutuk River (Tributary of Alatna River) Endicott Mountains, Alaska."

Microtus andersoni Rand, 1945a:42. Type locality "near headwaters of Little Keele River, 82 miles west of Mackenzie River on the Canol Road, Northwest Territories, Canada; altitude 5,500 ft."

Microtus cantator Anderson, 1947:161. Type locality "above timber-line on mountain top near Tepee Lake on north slope of St. Elias Range [Yukon, Canada; about latitude 61°35′N, longitude 140°22′W]."

Microtus miurus paneaki Rausch, 1950:135. Type locality "Tolugak Lake (lat. 68°24′N, long. 152°10′W), Brooks Range, Alaska."

Microtus gregalis miurus: Rausch, 1964:346. Name combination (see "Nomenclatural Notes").

CONTEXT AND CONTENT. Order Rodentia, family Cricetidae, subfamily Arvicolinae, subgenus indeterminate (Musser and Carleton 2005). Four subspecies were recognized by Lidicker and Batzli (1999):

M. m. cantator Anderson, 1947:161. See above.
M. m. miurus Osgood, 1901:64. See above.
M. m. muriei Nelson, 1931:311. See above (*andersoni* and *paneaki* are synonyms [see "Nomenclatural Notes"]).
M. m. oreas Osgood, 1907:61. See above.

NOMENCLATURAL NOTES. Classically, this species was included as a member of the subgenus *Stenocranius* by Miller and Kellogg (1955) and Hall (1981), an association intended to reflect a close affinity to the Old World narrow-headed vole (*Microtus gregalis*). *M. miurus* was synonymized with *M. gregalis* by Rausch (1964) and Rausch and Rausch (1968) to form a Holarctic species (Musser and Carleton 2005). However, Anderson (1960), Fedyk (1970), Gromov and Polyakov (1977), Hall (1981), and Vorontsov and

Fig. 1.—An adult *Microtus miurus miurus* from Alaska. Photograph courtesy of R. L. Rausch.

Lyapunova (1986) considered that the morphological similarities between these 2 species were the result of convergence rather than phylogenetic relationship, and argued that *M. miurus* was a distinct species with distant kinship to *M. gregalis*. Phylogenetic studies of chromosomes (Zagorodnyuk 1990) and mitochondrial DNA sequences (Conroy and Cook 2000; Jaarola et al. 2004) also supported this position. These studies prompted Musser and Carleton (2005) to remove both *M. miurus* and the insular vole (*M. abbreviatus*) from the subgenus *Stenocranius*. Earlier Zagorodnyuk (1990) had recognized this divergence by placing *M. miurus* in the subgenus *Alexandromys*. Conroy and Cook (2000) suggested that *M. miurus* and its sister species *M. abbreviatus* originated early in the radiation of North American *Microtus*, distinct from the Palearctic species. They also suggested that these 2 taxa may be conspecific.

Rausch (1950) described *M. miurus paneaki* based on specimens from the Anaktuvuk Pass region in the Brooks Range, Alaska. However, in a review of Nearctic *Microtus*, Hall and Cockrum (1952) concluded that *M. miurus paneaki* was conspecific with *M. miurus muriei*. Hall (1981) and Lidicker and Batzli (1999) agreed. After reviewing holotypes of *M. miurus* subspecies from Alaska and specimens from Canada, Hall and Cockrum (1952) tentatively concluded that there were no valid subspecies, but they retained 5 subspecies pending further study. Miller and Kellogg (1955) and Hall (1981) also retained these 5 subspecies. However, Lidicker and Batzli (1999) argued that *andersoni* (and *paneaki*) was of doubtful validity and should be synonymized with *muriei*.

Microtus miurus is a sibling species to *M. abbreviatus*, which is endemic to Hall and St. Matthew islands in the Bering Sea (Manville and Young 1965). Each island has its own subspecies: *abbreviatus* (Hall Island) and *fisheri* (St. Matthew Island). Adults of *M. abbreviatus* are brownish dorsally with pale yellowish sides, rump, tips of ears, face, and a buff-colored belly (Kays and Wilson 2002). *M. miurus* is smaller and tends to be slightly more buffy ventrally and on the dorsal surfaces of the tail and feet. These taxa were likely isolated from one another at the end of the Pleistocene by rising sea level (Conroy et al. 2001). Although currently recognized as distinct species (Musser and Carleton 2005), Conroy and Cook (2000) and Jaarola et al. (2004) suggested that these species might be conspecific based on their analysis of mitochondrial cytochrome-*b* divergence distances. In addition, the karyotypes of *M. miurus* and *M. abbreviatus* are the same in terms of diploid number of chromosomes (2n = 54) and the morphology of the various chromosome pairs, including the sex chromosomes (fundamental number = 72—Fedyk 1970; Rausch 1964; Rausch and Rausch 1968).

The common name of *M. miurus* is the singing vole. This species is also known as the Alaska haymouse, Alaska vole, Toklat vole, and campagnol chanteur (Banfield 1974; Lidicker and Batzli 1999).

DIAGNOSIS

Microtus miurus differs from other northern voles in combination of a buff-colored venter, a short tail, long claws, tops of the hind feet being cream colored, and an orange line on the lower sides (Kays and Wilson 2002). Other sympatric *Microtus* have white to gray venters, smaller claws, and longer tails. The western heather vole (*Phenacomys intermedius*) has longer whiskers than in *M. miurus* and other *Microtus* species. Pelage coloration also differs. The northern red-backed vole (*Myodes rutilus*) can be distinguished from *M. miurus* by its reddish to rusty colored back. The pelage coloration and grooved upper incisors distinguish the northern bog lemming (*Synaptomys borealis*) from *M. miurus*. Pelage coloration and greatly reduced tail length distinguish the Siberian brown lemming (*Lemmus sibiricus*) and the Nearctic collared lemming (*Dicrostonyx groenlandicus*) from *M. miurus*.

A sister relationship exists between *M. miurus* and *M. abbreviatus* (Conroy and Cook 2000). *M. abbreviatus* is very difficult to distinguish from *M. miurus* in pelage color and pattern (Rausch and Rausch 1968). However, *M. abbreviatus* is restricted to Hall and St. Matthew islands in the Bering Sea off the coast of Alaska (Manville and Young 1965).

GENERAL CHARACTERS

Microtus miurus is an average sized vole with small ears that are nearly concealed by hair, relatively long and narrow claws, and a short tail (Banfield 1974; Kays and Wilson 2002; Lidicker and Batzli 1999; Fig. 1). The pelage is dense, long, and soft. Pelage color is variable throughout the distribution, from pale buffy gray to pale ochraceous to pale tawny (Hall 1981). Some specimens are orange brown on the back and upper sides, whereas others are grayish brown (Banfield 1974; Kays and Wilson 2002; Osgood 1901). The intensity of brown pelage coloration increases moving east to west across the distribution range (Bee and Hall 1956). The characteristic markings for *M. miurus* include ochraceous buffy patch at base of the ears, along flanks, and on rump. There is frequently a buffy patch at the base of the fine, long vibrissae. The under parts are buff or ochraceous with gray underfur. Short and heavily furred, the tail is dusky above, clear buff or tawny beneath and on the sides, and tipped with stiff, buffy or tawny hairs. Stiff and buff to black-tipped guard hairs (15–16 mm) are sparse on the dorsal surface, barely darkening the color. Tail length is roughly equal to the length of the hind foot. The feet are heavily furred with creamy or pale buff hair extending beyond the tip of the claw.

Fig. 2.—Dorsal, ventral, and lateral views of skull and lateral view of lower mandible of *Microtus miurus miurus* (adult male, United States National Museum 159129) that was collected on 23 April 1908 at Alaska: Mt. McKinley Range; Head of Toplat River. Greatest length of skull is 27.5 mm.

The color of the preadult pelage is similar to that of the adult. The winter pelage coloration is typically paler and grayer (Bee and Hall 1956; Rausch 1964) than the summer pelage. The winter fur is also longer than the summer fur (Banfield 1974).

The skull of *M. miurus* is small and proportionally long and slender (Fig. 2). The skull is low in profile and the dorsal and ventral surfaces are roughly parallel (Osgood 1901). The interorbital region is narrow and uniform in width, slightly depressed in side view (Rausch and Rausch 1968). The rostrum is proportionately long and narrow. The nasals are moderate in length and flare slightly anteriorly. The dorsal outline of the skull is almost straight. The cranium is relatively small and narrow, flattened laterally with parallel sides; the auditory bullae are large, elongate-rounded, and their inner surfaces are almost parallel (Banfield 1974). The zygomata are rounded anteriorly and the arches are relatively slender and flattened laterally. The posterior ridge of the palate typically ends abruptly, forming a broad shelf rather than a keel (Rausch 1964). Subadult skulls have a smooth interorbital surface; however, a pronounced inter-orbital crest may be present in adults (Banfield 1974; Osgood 1901). Typically, the prezygomatic notch is absent or shallow in subadult skulls but conspicuous in adult skulls.

Given that adult voles keep growing and that seasonal shifts in age structure occur, it seems pointless to report all the measurements found in the literature for both sexes of each subspecies. Sexual dimorphism is slight and variation in size between the various subspecies is inconsistent, so measurement data are combined below.

Ranges for external measurements (mm) of *M. miurus* were: total length 95–161; length of tail 15–41; length of hind foot 14–22; and height of ear from notch 10–14. The range of weights for *M. miurus* studied was 11–60 g (Bee and Hall 1956; Hall 1981; Quay 1951; Rausch 1964; Rausch and Rausch 1968; Youngman 1975).

Ranges for cranial measurements (mm) of *M. miurus* were: condylobasal length 22.8–29.6; occipitonasal length 24.8–28.3; palatilar length 12.1–14.3; width of rostrum 4.5–5.9; zygomatic width 10.1–16.1; lambdoidal width 10.1–12.8; mastoid breadth 9.8–12.7; length of nasals 5.6–8.3; length of maxillary toothrow 5.2–7.0; length of incisive foramen 3.8–5.5; interorbital width 2.8–3.6; greatest width of braincase 10.7–12.7; distance between supratympanic fenestrae 8.0–9.3; and palatofrontal height 6.4–7.8 (Bee and Hall 1956; Rausch 1964; Rausch and Rausch 1968; Youngman 1975).

To give some idea of the amount of sexual dimorphism and geographic variation, we measured samples of the 2 most distinctive subspecies (*M. m. muiriei* and *M. m. oreas*). External measurements (mm) were taken by us from 10 male and 10 female specimens of *M. m. muriei* from the collection of the National Museum of Natural History, Washington, D.C. These voles were collected in mid-June 1951 near the mouth of the Anaktuvuk River, Alaska. The following measurements (means ± *SE* and ranges) were recorded for these males and females (in parentheses): total length 146.9 ± 2.1, 135–157 (148.8 ± 1.8, 140–157); length of tail 26.8 ± 0.9, 23–31 (28.5 ± 0.8, 25–33); length of hind foot 20.0 ± 0.2, 19–21 (19.7 ± 0.2, 19–20); and length of ear 12.3 ± 0.2, 11–13 (12.1 ± 0.2, 11–13). There were no significant differences between male and female measurements.

Cranial measurements (mm) for *M. m. muriei* also were taken from these 10 male and 10 female specimens. The

following measurements (means ± *SE* and ranges) were reported for males and females (in parentheses): condylobasal length 27.3 ± 0.2, 26.2–28.2 (26.8 ± 0.2, 26.3–27.8); length of nasals 7.3 ± 0.1, 7.0–7.9 (7.2 ± 0.1, 6.8–7.6); zygomatic width 13.8 ± 0.1, 13.2–14.1 (13.3 ± 0.2, 12.3–14.2); interorbital breadth 3.0 ± 0.1, 2.4–3.2 (3.0 ± 0.1, 2.7–3.4); breadth of braincase 9.7 ± 0.1, 9.2–10.5 (9.5 ± 0.1, 8.9–10.3); width of palate across molars 2.6 ± 0.05, 2.3–2.8 (2.5 ± 0.06, 2.3–2.7); length of maxillary toothrow 6.2 ± 0.1, 5.8–6.5 (6.2 ± 0.06, 5.8–6.5); length of mandibular toothrow 5.9 ± 0.1, 5.5–6.2 (5.9 ± 0.06, 5.6–6.3); breadth of rostrum 5.1 ± 0.1, 4.6–5.6 (4.9 ± 0.1, 4.3–5.5); and length of bulla 7.3 ± 0.1, 7.0–7.7 (7.1 ± 0.04, 6.8–7.2). Although the mean for most cranial measurements was greater for males than for females, only the length of the bullae was significantly greater for males.

External measurements (mm) for 10 male and 10 female *M. m. oreas* were taken from specimens in the collection of the National Museum of Natural History, Washington, D.C. These voles were collected in mid-June 1951 near Toklat River, Alaska. The following measurements (means ± *SE* and ranges) were recorded for males and females (in parentheses): total length 148.9 ± 1.8, 140–161 (145.6 ± 1.7, 140–156); length of tail 22.5 ± 1.2, 16–27 (24.7 ± 1.3, 21–34); and length of hind foot 20.7 ± 0.3, 20–23 (20.9 ± 0.2, 20–22). There were no significant differences between male and female measurements.

Cranial measurements (mm, means ± *SE* and ranges) taken from the same specimens (10 males and 10 females [in parentheses]) of *M. m. oreas* were: condylobasal length 26.9 ± 0.2, 25.4–27.9 (25.6 ± 0.3, 25.0–27.4); length of nasals 7.1 ± 0.2, 6.1–7.6 (6.8 ± 0.2, 6.2–7.7); zygomatic width 13.8 ± 0.3, 11.3–14.6 (12.3 ± 0.3, 10.8–13.9); interorbital breadth 3.1 ± 0.1, 2.7–3.6 (3.0 ± 0.04, 2.8–3.2); breadth of braincase 9.7 ± 0.2, 9.1–10.5 (9.4 ± 0.1, 9.1–10.0); width of palate across molars 2.3 ± 0.03, 2.2–2.5 (2.3 ± 0.03, 2.2–2.5); length of maxillary toothrow 6.3 ± 0.1, 5.9–6.7 (6.0 ± 0.1, 5.7–6.3); length of mandibular toothrow 5.9 ± 0.1, 5.6–6.3 (5.9 ± 0.1, 5.8–6.3); breadth of rostrum 5.0 ± 0.1, 4.5–5.7 (4.7 ± 0.1, 4.3–5.3); and length of bulla 7.9 ± 0.1, 7.5–8.3 (7.8 ± 0.1, 7.4–8.2). Condylobasal length, zygomatic width, breadth of braincase, length of maxillary toothrow, length of mandibular toothrow, and breadth of rostrum were significantly greater for male than for female *M. m. oreas*.

Mean tail length for male and female *M. m. muriei* (26.8 mm and 28.5 mm, respectively) is significantly longer than for male and female *M. m. oreas* (22.5 mm and 24.7 mm, respectively). Condylobasal length and width of palate at M3 were greater in *M. m. muriei* than *M. m. oreas* for both males and females. The length of the auditory bulla was significantly smaller for *M. m. muriei* than *M. m. oreas* for both sexes. Nasal length, zygomatic width, and length of the mandibular toothrow were
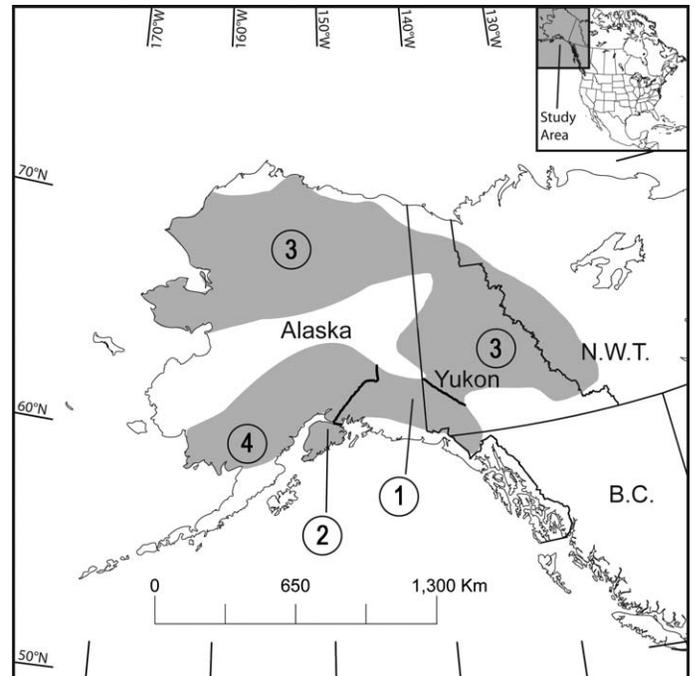

Fig. 3.—Geographic distribution of *Microtus miurus*. Subspecies are: 1, *M. m. cantator*; 2, *M. m. miurus*; 3, *M. m. muriei*; and 4, *M. m. oreas*.

significantly longer in female *M. m. muriei* than female *M. m. oreas*.

DISTRIBUTION

Microtus miurus is common in mountainous areas from the western coast of Alaska including the Seward Peninsula eastward through the Brooks Range into Canada to the Mackenzie Range, and southward to roughly 60°N (Rausch 1964). The northern limit of *M. miurus* occurs in the transition region between coastal plain and the foothills of the Alaskan ranges (Fig. 3). Pitelka and Batzli (1993) indicated that the northern limit for *M. miurus* was roughly the 200-m elevation line across the North Slope except along major river valleys where appropriate habitat may be present. Although Bee and Hall (1956) collected a few *M. miurus* on the coastal plain, widespread trapping by Pitelka and Batzli (1993) indicated that *M. miurus* was generally absent from coastal plain habitats. *M. miurus* is missing from the central portion of the state and the Alaska Pennisula. However, *M. miurus* is found through the Alaskan Range and Kenai Peninsula westward across the southern part of the state to the coast.

In Canada, the range of *M. miurus* includes much of the Yukon, continuing eastward into the western Northwest Territories, and southward to southwestern Yukon and extreme northwestern British Columbia (Banfield 1974; Martell and Pearson 1978; Musser and Carleton 2005).

FOSSIL RECORD

Fossil specimens of *Microtus miurus* have been reported from Alaska (Sullivan Pit, Fairbanks II, and Fairbanks I) and from the Yukon (Old Crow River Localities 11, 12, 14N; and Bluefish Cave I—Zakrzewski 1985). These sites range in age from Illinoian to Holocene and with the exception of the Sullivan Pit site *M. miurus* is not found near any of these sites today. The earliest fossil record for *M. miurus* is from Fairbanks I in Alaska (Zakrzewski 1985).

Repenning et al. (1964) reported that *M. miurus* is the best-represented rodent in the late-Pleistocene fauna of the Tofty placer district in central Alaska. Repenning et al. (1964) concluded that *M. miurus* might be the most sensitive indicator species of environmental conditions present in the late-Pleistocene rodent fauna of the Tofty area. Fossil remains from the earlier part of the late Pleistocene are not known.

There is evidence suggesting that the lineage leading to *M. miurus* reached East Beringia during the Illinoian glacial period. Zakrzewski (1985) suggested that the insular *M. abbreviatus*, the closest present-day relative of *M. miurus*, probably evolved from *M. miurus* in the Wisconsinan. However, based on mitochondrial cytochrome-*b* gene sequences, Conroy and Cook (2000) and Jaarola et al. (2004) suggested that *M. miurus* originated early in the radiation of North American *Microtus* and is morphologically convergent with the Palearctic species *M. gregalis*. Gromov and Polyakov (1992) indicated that the range of *M. miurus* once covered the Yukon depression and extended east of the Mackenzie River.

Woodman et al. (1996) reported that sediments at a site in Elkader, Clayton County, Iowa, contained evidence of a tundralike biota at this location, which included *Microtus* cf. *miurus*. Radiocarbon dating at this site indicated an age of about 20,530 years ago. Similar fossils have been recovered from southeastern Iowa (Baker et al. 1986; Foley and Raue 1987). Wallace (2001) also reported fossils of *M. miurus* from the upper Mississippi Valley in Iowa during the late Pleistocene.

FORM AND FUNCTION

Most *Microtus* possess a mean of 6 meibomian or tarsal glands. However, *M. miurus* possesses a mean of 9 meibomian or tarsal glands (Carleton 1985; Quay 1954). Quay (1954) studied the distribution of meibomian glands in a variety of voles and lemmings including *M. miurus*. He noted a mean of 7.5 meibomian glands in the dorsal lid (range 5–9) and a mean of 2.0 in the ventral lid (range 2–2) in the 4 *M. miurus* examined. He also noted that variation in meibomian gland number was not correlated with sex, season, or age.

Well-developed flank glands are present in most adult males and some lactating females (Quay 1968). These glands are externally undetected in immatures. These enlarged and modified sebaceous glands play an important role in visual and olfactory communication. Quay (1968) reported that the growth and sloughing of the epidermal cells on these glands is marked. He also suggested that there was a trend for greater gland development at more northerly latitudes within the genus *Microtus*.

There is a slight sexual dimorphism in *M. miurus* with males being slightly larger than females (Bee and Hall 1956; Lidicker and Batzli 1999). Individuals of *M. miurus* from the northern part of the range are somewhat larger than those from the south (Lidicker and Batzli 1999). In addition, Bee and Hall (1956) described differences in cranial size and shape for different cohorts of *M. miurus* on the Arctic Slope of Alaska (Carleton 1985). Individuals born in the late spring and summer have a narrower braincase and a longer skull length, and are generally larger than individuals born in the previous autumn or winter (Bee and Hall 1956). These differences may be the result of a better nutritional base and less stressful environmental conditions in the summer than in the winter.

The dental formula is i 1/1, c 0/0, p 0/0, m 3/3, total 16. *M. miurus* is characterized by relatively narrow molars and a distinctive enamel pattern, which it shares with *M. abbreviatus*. The upper incisors are slightly sulcate on the anterior surface. M1 has 5 or 6 closed triangles, and 5 inner and 4 outer salient angles. M3 possesses a strong tendency for 2 closed triangles, the 3rd triangle being open and confluent with the posterior loop. This molar enamel pattern is similar to that of *M. abbreviatus* and distinguishes these 2 species from other members of the subgenus *Microtus* (Osgood 1901; Rand 1945b; Rausch 1964).

Heske and Ostfield (1990) suggested that data related to sexual dimorphism and testis size may be used as indicators of mating systems in small mammals. They predicted that if males are significantly larger than females and the relative testis size is small, the species is probably polygynous. For *M. miurus murei*, body length (mean $\pm$ *SD*) of males (123.3 $\pm$ 4.9; $n = 44$) and females (115.9 $\pm$ 5.7; $n = 38$) yields a male:female body-size ratio of 1.06 (Heske and Ostfield 1990). The relative testis length was 0.09. Consequently, they predicted that *M. miurus* was likely to be polygynous. However, other workers suggested that *M. miurus* exhibits a promiscuous mating system (Lidicker and Batzli 1999).

The baculum of *M. miurus* is almost 3 mm in length, 1.5 times the greatest width and 3.5 times the greatest depth. The median process is ossified 40–60% the length of the stalk, laterally compressed, and is sometimes arched in the dorsoventral plane. Lateral processes are cartilaginous and slender, and basal tuberosities are well developed. Tuberosities are confluent posteriorly. The posterior profile of the baculum is smoothly rounded to trilobate with the curvature

typically acute at the point of greatest width. In proximal end-view, the baculum base is wider dorsally with deep dorsal concavity, shallow ventral concavity, and medial constriction that is 60% of greatest depth. The baculum is twice as wide as high at the midpoint of the stalk; at the tip the stalk is higher than wide and laterally inflated. In lateral profile, the stalks for most specimens are abruptly curved anterior to the point of greatest width (Anderson 1960).

Phalli of *M. miurus* are relatively long and slender, have well-developed lateral bacular processes (may be cartilaginous), and have complex urethral lappets (Hooper and Hart 1962; Lidicker and Yang 1986). Lidicker and Yang (1986) provided mean phallic measurements (mm) for *M. miurus* (*n* = 3): glans length (middorsally) 4.67; glans width 2.94; baculum length 3.52; proximal baculum length 2.49; distal baculum length 1.00; width of proximal baculum base 1.50; and width of distal baculum base 0.38. They reported that the bacular shape was fairly consistent in their specimens. However, they reported a less-attenuated tip to the distal element than described by Anderson (1960). Strong lateral bacular processes (osseous or cartilaginous) were present in some specimens. Lidicker and Yang (1986) reported the presence of 6 pairs of dentate papillae on the lateral aspect of the outer rim. Only tiny indistinct papillae were found dorsally and ventrally to these. The urethral lappets have 2 medial projections, but lack a deep medial cleavage indicated by Hooper and Hart (1962). Lidicker and Yang (1986) indicated the presence of a broadly based dorsal papilla with 2 spines plus several small dentate conules on the dorsal surface. Also, a shallow dorsal notch in the outer crater is consistently present.

Individuals of *M. miurus* born in the spring experience 4 pelage types by early winter: juvenile (nestling), post-juvenile, preadult, and winter adult (Bee and Hall 1956). If the individual lives to a 2nd winter it has 4 additional pelage types: breeding adult, postbreeding adult, late-summer adult, and winter adult. The juvenile pelage appears 1st on the top of the head and dorsal surface. The growth center moves laterally toward the ventral surface. The postjuvenile and subsequent molts begin on the sides and move both dorsally and ventrally, often ending at the top of the head (Bee and Hall 1956). The preadult pelage follows a growth pattern similar to that of the postjuvenile molt. The breeding adult, postbreeding adult, late-summer adult, and winter adult pelages radiate from several growth centers simultaneously. Often the new pelage appears last on the rump, perhaps because the flank glands slow the progress of hair growth. Bee and Hall (1956) indicated that specimens collected on 3 September at their study site had late-summer pelage but specimens collected on 26 October had winter pelage. The winter pelage is longer and paler than the summer pelage. The late-summer pelage is generally a darker brown than the breeding or post-breeding pelage.

ONTOGENY AND REPRODUCTION

Ontogeny.—Batzli and Henttonen (1990) defined 3 age categories on the basis of mean size at molting for wild-caught *Microtus miurus* at Toolik Lake, Alaska. They considered juvenile *M. miurus* to weigh less than 18 g, subadult voles to weigh 18–28 g for females and 18–30 g for males, and adult voles to weigh greater than 28 g for females and greater than 30 g for males.

Morrison et al. (1977a) provided weight data over time for 120 male and 88 female *M. miurus* maintained in a laboratory colony. Weights (g) for ages greater than 8 weeks were smoothed using moving 3-week averages. Data are weights by age (week number) for males and females (in parentheses): week 0–3.0 (2.8); week 1–6.7 (6.8); week 2–10.7 (11.0); week 3–14.4 (14.0); week 4–19.2 (18.2); week 8–25.4 (20.4); week 12–29.0 (22.0); week 16–32.4 (23.9); week 20–35.7 (25.7); week 24–38.6 (27.8); week 28–41.5 (28.8); week 32–43.4 (29.6); week 36–45.2 (32.2); week 40–46.9 (38.0); week 44–50.3; week 48–51.7; week 52–53.5; and week 56–55.1.

Reproduction.—The breeding season in Alaska and Canada extends from the end of May to September (Banfield 1974; Bee and Hall 1956). The testes reach maximum size by late June to early July, and typically regress after mid-August (Bee and Hall 1956). Females are seasonally polyestrous, enabling up to 3 litters to be born during the breeding season. The mean litter size is 8.2 (range 4–12; *n* = 46) at the height of the breeding season (Bee and Hall 1956). Both sexes typically breed in the summer of their 1st year (Lidicker and Batzli 1999). Although reproduction is most likely in late spring and summer, pregnancy may occur at any time of the year. It is unlikely that adults survive a 2nd winter.

Microtus miurus has a gestation period of 21 days, similar in length to the period (20–25 days) for many other microtines (Morrison et al. 1976). Females have the normal microtine pattern of 8 mammae. Lactational delay in gestation has been reported for some microtines but examination of data from Morrison et al. (1976) suggests that there is no lactational delay in *M. miurus*. *M. miurus* experiences a postpartum estrus shortly after giving birth. Youngman (1975) speculated that males might become sexually mature earlier than females based on observations from a laboratory colony and an analysis of weights of wild-caught individuals.

For *M. miurus* at Umiat, Wahoo Lake, Porcupine Lake, and Mount Mary, Alaska, testes had already reached maximum size in late June and early July (Bee and Hall 1956). The mean length of testes of adult breeding males caught between 25 June and 3 August was 11 mm (range 6–13 mm—Bee and Hall 1956). Between 10 August and 3 September at the Chandler Lake, Driftwood, and Umiat sites, the size of testes in breeding males was less, averaging 6.6 mm (range 5–9 mm). Overwintering males that were

breeding in the spring had smaller testes. The mean length of testes in subadults (total length 95–135 mm) from various localities on the North Slope was 2.8 mm (range 2–4 mm; n = 136); none of these animals appeared to be in breeding condition (Bee and Hall 1956).

Testes size was recorded by us from specimen tags for *M. miurus* in the National Museum of Natural History collection. These voles were caught in mid-June 1951 from Anaktuvuk River and Chandler River in Alaska. The mean testis size for these voles was 12 by 7 mm (n = 11). Pruitt (1966) reported testes length (mm) for *M. miurus* collected from Angmakrok Mountain in the Cape Thompson region of Alaska in 1959 (high population density) of 3 mm (n = 23), in 1960 (low population density) of 5 mm (n = 5), and in 1961 (population density increasing) of 4 mm (n = 17).

Bee and Hall (1956) reported that the mean number of embryos per female at the time of greatest reproductive activity was 8.2. No significant difference was observed between the mean number of embryos in the right (4.13) and left (4.10) horns of the uterus, although the size of some individual embryos varied considerably. The largest embryo measured from 46 pregnant females was 23 mm in crown to rump length. The smallest female bearing embryos was 131 mm in total length and the largest female was 162 mm in total length (Bee and Hall 1956). The mean total length for pregnant females in their sample was 147 mm. Examination of autopsy and trapping data indicated that young were still being conceived in late September at Anaktuvuk Pass, Alaska. Bee and Hall (1956) suggested that a few individuals reproduce between late summer and early spring. Timing of breeding differs with changes in elevation and exposure (Bee and Hall 1956).

Microtus miurus muriei collected in mid-June in the area near Anaktuvuk River, Alaska, had a mean litter size of 10.4 (range 8–14; n = 9) based on number of embryos or uterine scars. Near Toolik Lake, Alaska, *M. miurus* began breeding in the spring before snow melt was complete and was still breeding when the 1st heavy snows occurred in autumn (Batzli and Henttonen 1990). Adult *M. miurus* showed greater reproductive intensity and had larger litter sizes than did young voles. Batzli and Henttonen (1990) reported that mean litter size ($\pm$ *SE*) for adult *M. miurus* was 8.4 $\pm$ 0.4 (n = 12) and 6.4 $\pm$ 0.5 (n = 11) for subadults.

ECOLOGY

Population characteristics.—The sex ratio for *Microtus miurus* based on trapping data from Umiat, Wahoo Lake, Porcupine Lake, and Mount Mary, Alaska, was approximately 50:50 in the spring, but by late summer the ratio was biased toward females, probably the result of greater exposure of males to predators, fighting among males, and other ecological factors (Bee and Hall 1956). However, the

sex ratio of subadults remained approximately 50:50 throughout the summer.

Populations of *M. miurus* fluctuate widely in numbers. Pruitt (1966) found *M. miurus* to be the 2nd most common rodent living at his study site on Angmakrok Mountain in the Cape Thompson region of northwestern Alaska. The number of voles decreased from 51 animals in 1959 to 1 in 1961, indicating that *M. miurus* undergoes large fluctuations in population size in that area. However, Douglass (1984), working in foothill tundra in the De Long Mountains, reported that densities of *M. miurus* obtained by livetrapping remained low during his 2-year study (1978–1979), roughly 0–7 voles per hectare.

Batzli and Henttonen (1990) studied populations of *M. miurus* near Toolik Lake, Alaska, from 1984 to 1987 where this species was widespread and abundant. Population densities of *M. miurus* varied from 5 to almost 50 per hectare over the 4 years of their study. Within their preferred habitats, densities of *M. miurus* varied synchronously during the study. Batzli and Henttonen (1990) noted a shift from adult-dominated populations in the early summer to immature-dominated populations in the late summer. They also noted reduced body weight and poor reproduction as densities declined, population characteristics typically associated with population cycle declines (Lidicker and Batzli 1999).

Although they did not trap in the alpine areas of the northern St. Elias Mountains in Yukon and eastern Alaska, Murray and Murray (1969) reported extensive signs of *M. miurus* (e.g., calling, high burrow density, and haypiles) in 1967. By June of the following year, the population appeared to have crashed. They also noted that regionally, populations of *M. miurus* appeared to be asynchronous. Childs (1969), working in the Pitmegea River region of Cape Sabine in northwestern Alaska, observed that population densities of *M. miurus* appeared high in autumn of 1957 when sign was abundant. The population crashed over the winter, and abundance was low in 1958. Both studies indicated that populations of *M. miurus* can undergo strong population fluctuations.

Krebs and Wingate (1985) assessed the population abundance of small rodents in subalpine and alpine tundra habitats of the Kluane Lake region, southwestern Yukon, from 1973 to 1977 using snap-trap lines. Captures of *M. miurus* increased from 14 in 1973 to a high of 30 in 1975, then declined to 2 in 1976 and 0 in 1977. *M. miurus* was the only vole they studied that did not seem to fit the pattern of attaining a peak density in 1973. *M. miurus* in this study did not show the body weight changes or any sign of variation in reproductive rates typical of cyclical species. *M. miurus* approximated 5% or less of the total captures of voles and mice in their study. Galindo and Krebs (1985) investigated population dynamics of *M. miurus* in the same areas during the summer of 1981. They reported that density was very low in June, increased through the summer, and reached a

density of 37 voles per hectare by the 1st week of September when trapping ended. They noted that 2 litters were produced during the breeding season, 1 in mid-June and 1 in mid-July.

Pitelka and Batzli (1993) analyzed microtine population fluctuations at 12 locations on the North Slope of Alaska. They questioned whether population cycles of *M. miurus* took place at Cape Sabine in northwestern Alaska. However, they believed that *M. miurus* experienced population cycles at some locations within its range (e.g., Toolik Lake and Umiat—Batzli and Henttonen 1990; Pitelka and Batzli 1993). Pitelka and Batzli (1993) suggested that microtine populations that reached high densities are likely to cycle. Although sychronony of microtine population fluctuations at particular sites might occur (Batzli and Henttonen 1990), Pitelka and Batzli (1993) found little support for general synchrony of microtine population fluctuations in northern Alaska.

Space use.—*Microtus miurus* is found in mountainous areas where it typically inhabits arctic and alpine tundra, willow thickets, spruce forests, and areas along riverbanks, lakeshores, and gravel beds (Banfield 1974; Bee and Hall 1956; Manville and Young 1965). *M. miurus* may live in areas that are snow covered for 8 months or more per year, in part by provisioning stores of food underground and in haypiles located above ground.

Pruitt (1966) found *M. miurus* to be restricted in its local distribution in the tundra region west of the De Long Mountains in northwestern Alaska, especially in willow thickets on river floodplains, other brushy areas, and stream banks where winter snow cover is likely high. Working in foothills tundra in same region, Douglass (1984) also caught *M. miurus* frequently in riparian grass–willow, sedge–willow meadows, and creek-bottom habitats. Moderate but substantial accumulation of litter characterized the habitat occupied by these voles. Childs (1969) found *M. miurus* to be common along wet drainage areas of the Pitmegea River in northwestern Alaska.

Quay (1951), working on the Seward Peninsula, found that *M. miurus* avoided wet areas where standing water was present and preferred adjacent moist tundra. Typical habitats where *M. miurus* were taken included moist areas on solifluction terraces on the lower slopes of hills and ridges, moist areas along the tops of lake and river banks, peat mounds and other small areas of raised ground surrounded by wet tundra, and dryer areas bordering swales and extensive marshes. *M. miurus* was scarce on the higher tundra slopes where cottongrass tussocks were common (Quay 1951).

Bee and Hall (1956), Batzli and Henttonen (1990), and Pitelka and Batzli (1993) also noted that populations of *M. miurus* studied on the North Slope of Alaska inhabited neither the wettest nor the driest habitats. *M. miurus* was typically found in mesic habitats where graminoids, forbs, horsetails, and low deciduous shrubs were common (Batzli and Henttonen 1993). Stream, river, and lake banks, especially where both a shrub overstory and herbaceous understory occur, were commonly frequented habitats on the North Slope. Habitat preferences of *M. miurus* found south of the Brooks Range are less clear (Douglass 1984; Krebs and Wingate 1976).

Batzli and Henttonen (1990) used topography and vegetational composition to identify 8 habitat types found along moisture gradients near Toolik Lake, North Slope, Alaska: 1) swales—wet sedge meadows in low areas with standing water; 2) watercourses—willows and sedges in drainage areas with ephemeral or permanent streams; 3) transition areas—between wet and better-drained habitat; 4) low slopes—moist, mossy slopes with sedges, forbs, horsetails, and shrubs; 5) steep slopes—better-drained, shrub-covered slopes; 6) rock flats—low areas near streams with patches of soil and vegetation (shrubs and horsetails) on large rocks; 7) tussock tundra—upland tundra with continuous vegetation composed of sedges, forbs, and shrubs; and 8) heaths—upland tundra with sparse cover of lichens and evergreen shrubs on gravel moraines. Batzli and Lesieutre (1991) reported that populations of *M. miurus* were most abundant in mesic habitats (habitats 4, 5, and 6), where preferred diet items (horsetails, palatable forbs, or deciduous shrubs) and ample cover were present. *M. miurus* was found at low densities in transitional areas between wet and mesic or dry and mesic habitats (habitats 2, 3, and 7), and were not collected in the wettest or driest habitats (habitats 1 and 8). Batzli and Lesieutre (1991) concluded that availability of high-quality food (especially highly palatable horsetail) is an important determinant of the relative abundance of *M. miurus* in different habitats. Their regression analyses noted positive population effects for 2 general indices of ground cover (total biomass and litter), which might indirectly reflect exposure to predators (Batzli and Lesieutre 1995). Experimental removal of cover had a significantly negative effect on populations of *M. miurus*.

Galindo and Krebs (1985) investigated the habitat preference of *M. miurus* in the ecotone between alpine tundra and subalpine shrub tundra in the Kluane Ranges in southwestern Yukon. Patches of shrubs and open meadows characterized this ecotone. *M. miurus* occurred primarily in open alpine tundra meadows. Dwarfed vascular plants, moss, and lichens dominated the alpine tundra habitat above 1,500 m in this area. *M. miurus* also was caught at the ecotone with the shrub-dominated habitat, but not in the subalpine shrub habitat. *M. miurus* was captured more frequently at live-trap stations surrounded by little to no shrub cover (25%). Few voles were caught in traps set under more than 50% shrub cover. Gilbert et al. (1986), working near Kluane Lake, found *M. miurus* where spruce trees were small, shrubs were sparse, and ground cover of moss was extensive. Krebs and Wingate (1976) reported collecting *M. miurus* mainly from alpine tundra, but also from marshes and spruce forest habitats in this area.

Diet.—*Microtus miurus* feeds primarily on grasses and sedges, horsetails, forbs (e.g., lupine, arctic locoweed, and knotweed), and shrubs (e.g., dwarf arctic willows—Banfield 1974; Batzli and Henttonen 1990; Lidicker and Batzli 1999). Quay (1951) identified leaves of *Carex* and leaves of *Petasites frigidus* as food items of *M. miurus*. He also noted *Carex nesophila* and *Artemesia arctica* were often observed clipped along runways. In autumn, *M. miurus* caches large amounts of food for winter use.

Batzli and Henttonen (1990) investigated the food habits of *M. miurus* collected near Toolik Lake, Alaska. In midsummer, horsetail comprised roughly 60% of the diet of *M. miurus*. Dicotyledons comprised 25–30% of the diet. Mosses, fruit, and seeds were small parts of the vole diet throughout the summer. *M. miurus* living in moist habitat during summer took fewer monocotyledons (19% versus 26%) and fewer dicotyledons (45% versus 62%) but more horsetails (31% versus 9%) than voles living in drier habitat (Batzli and Henttonen 1990). In September, *M. miurus* took dicotyledons (65% of diet) and monocotyledon shoots (30% of diet). *M. miurus* selectively forages on foods that provide high nutritional quality (e.g., shoots of forbs and leaves of deciduous shrubs—Batzli and Lesieutre 1991).

Stomach content analysis indicated that dicotyledons and horsetails contributed most to the summer diet for *M. miurus* (Batzli and Henttonen 1990). As winter approaches, the above ground portions of horsetails and monocotyledons die back. Then *M. miurus* takes more dicotyledon leaves and green bases of grass shoots. These differences in food selection appear to reflect strong dietary preferences because they are maintained in the transitional habitats. The food species preferred in the field were the ones that were most palatable in the laboratory. Batzli and Lesieutre (1991) suggested that the availability of high-quality food fostering high reproductive success might be a major factor affecting patterns of microtine distribution. Additionally, the preference for willows, forbs, and horsetails by *M. miurus* was not the outcome of competitive interactions with the often-sympatric root vole (*M. oeconomus*—Batzli and Lesieutre 1991).

Batzli and Lesieutre (1991) employed feeding trials in the laboratory to investigate the palatability and quality of 25 species of vascular plants in northern Alaska. *M. miurus* ate more and grew better on the shoots of forbs and leaves of deciduous shrubs. These food items were abundant in the mesic habitats preferred by these voles. The food items taken by *M. miurus* in the field also were the most palatable based on the results of laboratory feeding trials and the highest quality measured by physiological performance. Batzli and Lesieutre (1991) argued that *M. miurus* forages selectively on higher quality foods.

Based on laboratory feeding trials, the top 7 highest palatable food items listed in order of their palatability were *Equisetum arvense*, *P. frigidus*, *Polygonum bistorta*, *Salix glauca*, *Eriophorum angustifolium*, *S. reticulata*, and *Arctostaphylos rubra*; and the top 3 moderately palatable food items listed in order of their palatability were *S. pulchra*, *Epilobium latifolium*, and *Dodecatheon frigidum* (Batzli and Lesieutre 1991). High palatability was correlated with high quality as measured by maintenance or growth performance in young voles. Batzli and Lesieutre (1991) concluded that the availability of high-quality food determines, in large part, the relative abundance of microtine rodents in different habitats through a positive effect on reproduction (high birth rates).

Diseases and parasites.—Ectoparasites recorded for *Microtus miurus* belong to the orders Acari (mites and ticks), Anoplura (sucking lice), and Siphonaptera (fleas—Timm 1985). Rausch (1964) reported the tick *Ixodes angustus*. Quay (1951) found lice (*Polyplax alaskensis*) parasitizing *M. miurus* and also reported mites (*Acarina*) collected from *M. miurus oreas*. Fleas (*Amalaraeus dissimilis*, *Corrodopsylla curvata*, *Malaraeus penicilliger*, *Megabothris calcarifer*, *Megabothris groenlandicus*, *Megabothris quirini*, and *Peromyscopsylla ostsibirica*) also have been reported for *M. miurus* (Hopla 1965; Rausch 1964; Timm 1985).

Endoparasites reported for *M. miurus* belong to Cestoda, Nematoda, and Trematoda (Timm 1985). Seven species of Cestoda have been documented for *M. miurus*: *Paranoplocephala infrequens*, *P. omphalodes*, *P. borealis*, *P. batzli*, *Andrya arctica*, *Hymenolepis horrida*, and *Taenia mustelae* larvae (= *Taenia tenuicollis*—Doran 1954; Haukisalmi et al. 1995, 2004, 2006; Rausch 1952; Schiller 1952). Haukisalmi et al. (1995) reported that *P. omphalodes* and *P. batzli* (Cestoda: Anoplocephalidae) were relatively common endoparasites (13% and 7% of specimens, respectively; *n* = 182) of specimens of *M. miurus* collected at Toolik Lake, Alaska. Abundance of *P. batzli* was higher in overwintered males (up to 60%) than in other subgroups, probably the result of lower resistance in these animals from increased exposure during the winter (Haukisalmi et al. 1995).

Haukisalmi et al. (1995) also reported *P. arctica* and *Anoplocephaloides* cf. *variabilis* (Cestoda: Anoplocephalidae) from the small intestine of *M. miurus*; *A. troeschii* (Anoplocephalidae) from both the stomach and small intestine was relatively common (10% of specimens, *n* = 182); *H. horrida* (Hymenolepididae) from the small intestine; and larval *T. mustelae* (Taeniidae) from the lung. Habitat (wet versus dry) of *M. miurus* did not significantly impact the occurrence of the common cestodes. However, sex, age, and breeding condition did show significant effects on the occurrence of *P. omphalodes*. Haukisalmi et al. (1995) speculate that differential mortality of subgroups of *M. miurus* might be due, at least in part, to parasite loads and differential vulnerability to these parasites.

Doran (1955a) reported *Rictularia microti* (Nematoda) from specimens of *M. miurus paneaki*. *Syphacia* (Oxyuridae) was typically very abundant (> 100—Haukisalmi et al. 1995). *Mastophorus muris* (Spiruridea) from the stomach and *Heligmosomum* (Heligmosomidae) from the small intestine were less common in the specimens studied. Timm

(1985) lists 2 additional Nematoda from *M. miurus*: *Heligmosomum nearcticum* and *Trichinella spiralis* (= *T. nativa*).

Brachylaima rauschi and *Quinqueserialis quinqueserialis* (Trematoda) have been reported for *M. miurus* (Doran 1955b; Haukisalmi et al. 1995; Rausch 1952). Haukisalmi et al. (1995) identified *Q. quinqueserialis* (Notocotylidae) from the caeca of 7% (*n* = 182) of the *M. miurus* studied.

The blood parasite fauna of small mammals is relatively poor in arctic areas, possibly due to the lack of vectors (Fay and Rausch 1969). Nevertheless, Laakkonen et al. (2002) detected meronts of *Hepatozoon* in the lungs of a few *M. miurus* from Toolik Lake, Alaska. Laakkonen et al. (2002) did not find blood parasites in the heart, liver, spleen, or kidney, and suggested that fleas (e.g., *Amalaraeus dissimilis* and *Peromyscopsylla ostsibirica*) may be possible vectors of blood parasites in this area. Laakkonen et al. (2005) reported *Trypanosoma* in blood smears from *M. miurus* captured in Gates of the Arctic National Park in northern Alaska. They also reported collecting the flea and possible blood parasite vector *A. dissimilis* from *M. miurus* at this site.

Interspecific interactions.—*Microtus miurus* is associated with a number of microtine species across its wide ecological distribution (Bee and Hall 1956). Youngman (1975) reported *M. miurus* living in association with *M. oeconomus* and *Myodes rutilus* at his study site in the northern Yukon in montane habitats where their populations overlap.

Pruitt (1966) found *M. miurus* to be the 2nd most common microtine in the tundra region west of the De Long Mountains in northwestern Alaska. The 3 microtines found in the area (*M. rutilus*, *M. oeconomus*, and *M. miurus*) appeared to segregate habitats along a moisture gradient. *M. rutilus* occupied the driest habitats, *M. oeconomus* occupied the wettest, and *M. miurus* occupied the mesic habitats. This pattern of habitat segregation broke down as the summer progressed, with *M. rutilus* eventually occupying all habitats. Habitat use by *M. oeconomus* and *M. miurus* was similar, but only during midsummer.

Along the borders of swales and where canyon sides met wet meadows, populations of *M. miurus* invaded the areas inhabited by *M. oeconomus* but populations of *M. oeconomus* seldom entered the mesic communities preferred by *M. miurus* (Bee and Hall 1956; Pruitt 1966; Youngman 1975). These 2 species also met along eroded banks on the shores of lakes, where *M. oeconomus* occupied wet grasses at the base of the bank and *M. miurus* occupied the higher, drier slopes and flat area at the top of the bank. Douglass (1984) characterized habitat selection by *M. miurus* in comparison to *M. oeconomus* as higher maximum vegetation height; higher percent cover of grasses, herbs, and crowberry; and lower percent cover of litter, lichen, birch, sedge, and low willow.

Batzli and Lesieutre (1995) investigated the organization of the microtine rodent community found near Toolik Lake, Alaska. *M. oeconomus* and *M. miurus* were the most abundant and widespread microtines in this area. *M. rutilus*, *Lemmus sibiricus*, and *Dicrostonyx groenlandicus* also were present, but in low numbers (Batzli and Lesieutre 1995). Batzli and Henttonen (1990) reported that *M. miurus* reached similar densities to *M. oeconomus* in the study area. Population fluctuations in these 2 species appeared to be synchronous during the study, suggesting that similar environmental factors might control their densities. Populations of *M. miurus* were negatively associated with populations of *M. oeconomus*, probably because of their very different habitat preferences. Populations of *M. miurus* showed no response to supplemental feeding, but removal of shrub cover produced a clear negative response. *M. miurus* also showed a negative response to the removal of *M. oeconomus*, probably related to an indirect effect of increasing the probability of predation on *M. miurus*. Differences in food preference and habitat use between these 2 species suggest that competitive interactions are not a major factor influencing their abundance (Batzli and Lesieutre 1991). Batzli and Lesieutre (1991) concluded that community organization of microtine rodents near Toolik Lake is strongly influenced by availability of preferred foods and by predation, but less so by interspecific competition.

Myodes rutilus dominated the microtine community of the Kluane region in the southwestern Yukon (Krebs and Wingate 1976). *M. oeconomus* and *M. miurus* were common in some habitats. Other microtines taken in low to very low numbers included *Phenacomys intermedius*, the meadow vole (*Microtus pennsylvanicus*), the long-tailed vole (*M. longicaudus*), *Lemmus sibiricus*, and *Synaptomys borealis*. Gilbert et al. (1986) investigated activity patterns of *M. rutilus* and *M. miurus* seeking evidence of temporal separation of activity to avoid competition. Both species are active throughout the day, but there was no evidence of activity patterns being influenced by interspecific competition.

Galindo and Krebs (1985) investigated the habitat preference of *M. miurus* and *M. oeconomus* in the ecotone between alpine tundra and subalpine shrub tundra in the Kluane Ranges in southwestern Yukon. Removal of *M. oeconomus* from the habitat had no apparent effect on the distribution of *M. miurus*. Galindo and Krebs (1985) concluded that habitat distribution of *M. miurus* is not influenced by competitive interactions with *M. oeconomus*. Quay (1951) and Krebs and Wingate (1985) suggested that *M. miurus* has a narrow habitat niche breadth and a low niche overlap in comparison to the other species studied.

Numerous mammalian predators hunt *M. miurus*, including the grizzly bear (*Ursus arctos*), wolf (*Canis lupus*), wolverine (*Gulo gulo*), arctic fox (*Vulpes lagopus*), red fox (*Vulpes vulpes*), ermine (*Mustela erminea*) and least weasel (*Mustela nivalis*—Batzli and Henttonen 1990; Batzli and Lesieutre 1995; Bee and Hall 1956; Lidicker and Batzli 1999). The larger carnivores will disturb soil around burrow entrances by digging while hunting for voles. If not captured, voles will reestablish burrows and chambers.

Long-tailed jaegers (*Stercorarius longicaudus*) and pomarine jaegers (*Stercorarius pomarinus*) often cruise over mountain slopes and tundra habitat hunting voles (Batzli and Lesieutre 1995; Lidicker and Batzli 1999). The rough-legged hawk (*Buteo lagopus*) is a predator of *M. miurus* on Seward Peninsula (Springer 1975). The northern hawk owl (*Surnia ulula*) is a likely predator especially during periods of high population abundance in the southern part of the species' range (Rohner et al. 1995). Other avian predators (Banfield 1974; Lidicker and Batzli 1999) include gray jays (*Perisoreus canadensis*), short-billed gulls (*Larus canus brachyrhynchus*), herring gulls (*Larus argentatus*), short-eared owls (*Asio flammeus*), and snowy owls (*Bubo scandiacus*).

HUSBANDRY

Rausch (1953) reported some success in raising *Microtus miurus* in captivity. Continuous illumination with a 100 W incandescent bulb appeared to facilitate reproduction. His observations were based on 1 litter of 8 young. He reported that young weighed 2.0–2.8 g at birth and grew an average of 2 g per day for the first 20 days. These animals took solid food at 12 days of age and had a mean weight of 7.6 g. These animals showed the 1st signs of sexual activity 33 days after birth. The original breeding pair produced 2 additional litters (litter sizes of 6 and 7 voles) at roughly 3-week intervals.

Youngman (1975) reported observations from a captive colony of *M. miurus*, including a gestation period of 21 days. Postpartum estrus was common. Seventeen young were born during the observation period. Mean weight at birth was 2.3 g (range 1.7–3.0 g) and mean weight gain per day was 0.9 g/day (first 18 days) and 0.6 g/day (days 30–60). The eyes opened at roughly 12 days. Sexual activity occurred for 1 male at 24 days. Several other males became sexually active by the age of 34 days. One female became sexually active at 41 days and no females gave birth before 6 months of age.

Morrison et al. (1976, 1977a, 1977b) maintained a colony of *M. miurus muriei* under standard conditions of 20°C and 16 h of artificial light and 8 h of darkness. Voles were maintained as mated pairs or singly. Animals were kept in plastic boxes (20 by 20 by 90 cm) with bedding of wood shavings and nesting material composed of facial tissues. Bedding material was changed weekly. Food and water were provided ad libitum. Voles were bred at a minimum age of 2 months. Young were weaned at 4 weeks of age or upon the birth of a new litter. Eighty-three percent of the mated pairs (*n* = 52) reproduced (Morrison et al. 1976). Mean litter size at birth was 3.9 and the minimum time between litters was 21 days. Postpartum breeding occurred in 59% of the females.

Based on data gathered from a laboratory colony of *M. miurus*, Morrison et al. (1977b) indicated that the median life span was 43 weeks and the maximum life span was 112 weeks. The neonatal mortality rate (percent dying in the 1st week of life) was 16% and the infant and juvenile mortality rate (percent dying during the first 4 weeks of life) was 25%. The percent mortality within the 1st year of life was 86%.

BEHAVIOR

Based on his analysis of trapping data, Pruitt (1966) suggested that *Microtus miurus* exhibited aggregations, but he was unclear whether these groupings were true social aggregations or aggregations caused by habitat restrictions. Observations of captive *M. miurus* led him to support the social aggregation hypothesis. Quay (1951) reported typically finding *M. miurus* in groups of 1 adult and several subadults, and concluded *M. miurus* was markedly colonial. However, Lidicker and Batzli (1999) suggested that *M. miurus* was semicolonial. *M. miurus* is thought to nest communally and to overwinter in family groups (Murie 1961), but this remains to be substantiated (Lidicker and Batzli 1999). *M. miurus* swims well and climbs among low branches of willows (Banfield 1974). *M. miurus* is active 24 h per day as well as throughout the year in the field. In captivity, there is a peak in wheel-running activity at about midnight (Swade and Pittendrigh 1967).

Many species of *Microtus* possess enlarged and modified sebaceous glands, which are used for scent marking (Carleton 1985; Wolff 1985). These glands are present on the flanks of both male and female *M. miurus*. The flank glands are most prominent on the males during the breeding season. Scent marking appears to be used for individual recognition, indicating reproductive condition, and for marking territory boundaries. Males appear to mark more frequently than females. When modified sebaceous glands become hypertrophied, sexually aroused males scratch them with their hind legs to stimulate secretion of sebum, which is then rubbed on objects in their environment. Females appear to determine the breeding condition of males by smelling their flank glands and males appear to determine the breeding condition of females by smelling their perineal region (Youngman 1975). *M. miurus* also communicates through the creation and placement of scat piles or latrine sites (Murie 1961).

Like many microtines, *M. miurus* constructs runway systems, although its surface runways are not as pronounced as for some other voles (Murie 1961; Wolff 1985). Runways are constructed in well-drained soil or under rocks, and are typically intersected by branches leading to feeding areas (e.g., haypiles) and nesting–resting areas. Bee and Hall (1956) noted that runways of *M. miurus* often cross those of arctic ground squirrels (*Urocitellus parryii*). *M. miurus* may use abandoned ground squirrel burrows (Murie 1961).

Rand (1945b), working in the Northwest Territories, Canada, reported multiple (a few to 12) burrow entrances within a few square meters, each conspicuous because of dirt piled around it. Voles form these piles by carrying small pellets of excavated soil in their mouths to the surface and

dumping them around the burrow entrance (Murie 1961). Bare areas up to 0.5 m^2 may be created in this way. Burrow entrances are normally horizontal to the ground rather than oriented vertically on a slope (Osgood 1901) and burrows are roughly 2.5 cm in diameter. Murie (1961) found no burrows longer than roughly 1 m and no more than 20 cm below the surface. Food storage chambers were often located a short distance inside some of the burrows. Additional burrows extend through the soil, some ending in nest chambers containing shredded vegetation for bedding.

Murie (1961) described tunnels of *M. miurus* as a series of cavities separated by narrow apertures barely large enough to allow the vole to pass through. These constrictions were most numerous in tunnels leading to nesting chambers and less common in tunnels leading to food caches. Murie (1961) speculated that these constrictions served to slow weasel movement through the tunnels, increasing the chances for vole escape. Passageways to food caches seem simple with no constrictions to hamper food storage.

Batzli and Henttonen (1993) used intensive livetrapping over 4 summers (1984–1987) near Toolik Lake, Alaska, to determine that population density and season (early or late growing season) did not influence the home-range size of *M. miurus*. However, home-range size increased with body size for both sexes, with adult males generally having larger home ranges than adult females (mean areas of 1,250 and 450 m^2, respectively).

The high degree of overlap of home ranges of reproductively active females by multiple male home ranges suggests that females accept multiple mates (Batzli and Henttonen 1993). Additionally, the larger male home ranges suggest that males are promiscuous and seek multiple females for mates. Home ranges of same-sex individuals overlap far less than home ranges of individuals of the opposite sex. Batzli and Henttonen (1993) suggested that territorial behavior changes as the breeding season progresses. In their study, males tended to be territorial early in the breeding season and females became territorial late in the breeding season.

Working in the Alaskan range, Murie (1961) reported *M. miurus* storing roots, rhizomes, and other food items underground. Underground storage chambers were approximately 25–45 cm long, up to 25 cm wide, and 12–15 cm deep. Often only 10–20 cm of soil and sod covered these chambers (Banfield 1974; Rand 1945b). Many of the chambers that were excavated were partially filled with food (e.g., rhizomes of *Carex*; horsetail tubers; root fragments of *Hedysarum*, *Pedicularis*, and *Polygonum*; buds and roots of *Petasites*; and grass buds and shoots). Murie (1961) reported finding several of these storage chambers in close proximity, suggesting that the same group of voles may provision multiple chambers in preparation for overwintering. Roots appear to be harvested by digging from the surface (e.g., *Pedicularis*, *Polygonium*, and sedges) or by tunneling through the ground (e.g., fireweed [*Epilobium latifolia*],

sandalwood, horsetail [*Equisetum*], and coltsfoot [*Petasites*]). Root storing seemed at its height in late September after haymaking had declined (Murie 1961). In the autumn and spring, grizzlies may uncover and deplete vole food storage chambers while searching for food. Lidicker and Batzli (1999) speculated that the underground storage chambers observed by Murie (1961) might have been constructed by *M. oeconomus* rather than *M. miurus*.

Many arvicoline species hoard food, but most do so underground. *M. miurus* is distinctive because it builds haypiles above ground as well as hoarding food underground. The construction of haypiles in August may be triggered by low temperature accompanied by rain or snow (Murie 1961). An interesting feature of haymaking by *M. miurus* is the apparent care these voles take to keep the hay dry (Murie 1961). Different strategies are employed to keep the hay off the ground and allow it to dry. Often hay is piled among branches of low-lying dwarf birch or willow, which serve as a crib to keep the hay off the damp ground. On open ridges, cuttings may be layered over rocks for drying before being cached underground. In woods, hay is often piled against a tree trunk, but on an exposed root buttress rather than the ground. Bee and Hall (1956) noted that some haypiles were constructed under overhanging rocks, probably to protect the harvest from rain. Often subterranean storage chambers were associated with piles placed under rocks but not with piles placed in other locations (e.g., bases of shrubs). Only green vegetation is cut and spread in a layer to cure. Once the layer is dry, another layer is added. Bee and Hall (1956) suggested that *M. miurus* uses *Equisetum*, if available, as a basal platform and for alternate layers to aid aeration of the pile. The resulting haypile is sufficiently dry not to mold (Murie 1961). Batzli and Henttonen (1993) found that the nutritional quality, especially the nitrogen content, of haypile components was higher than in uncut senescent shoots. These haypiles provide winter forage with higher protein content and were built primarily in the home ranges of immature animals, the only cohort to survive over the winter (Batzli and Henttonen 1993).

Typically, hay making begins in early August and is near completion by the end of the month. Murie (1961) noted that at his Lake Peters study site the most active periods of building haypiles were before and after the 1st snows (10–15 August). Youngman (1975) reported haypiles being built in northern Yukon also in early August. At 1 site, Murie (1961) counted 49 haypiles ranging in volume from 1 to 13 l in an 800-m^2 area. The largest of these haypiles was 45 cm in diameter at the base and 50 cm high. He observed 2 piles being built over 2 days, 1 was roughly 4 l in volume and the other 3 l. Although piles can be built in a few days, normally the task takes 2–3 weeks. Bee and Hall (1956) witnessed 13 voles each apparently constructing separate haypiles in a 10 by 13-m area.

Haypiles may consist of fireweed (*E. latifolia*), horsetail (*Equisetum*), coltsfoot (*Petasites*), willow (*Salix*), mountain

avens (*Dryas*), lupine (*Lupinus*), and sage (*Artemisia hookerianna*—Murie 1961). Smaller amounts of pyrola (*Pyrola*), arctous (*Arctous*), and alder (*Alnus*) were sometimes present. Grass (*Calamagrostis canadensis*) was occasionally stored and dominated a few piles. Haypile composition reflected availability of food items. Some piles were composed of many food items but others contained only 1 or a few species (Kays and Wilson 2002; Murie 1961; Wolff 1985). One pile studied by Bee and Hall (1956) contained by volume, *Aster sibericus* (1%), *Salix reticulatus* (1%), *Lupinus* (5%), *Petasites hyperboreus* (10%), *Astragalus umbellatus* (10%), *Equisetum* (30%), and *Salix* (42%).

Murie (1961) reported observing haypiles in a variety of places including from ephemeral stream bottoms to ridge tops and dense spruce forest to open tundra. Some piles were built over a pile from the previous year. Cuttings ranged in length up to 38 cm and were often made within 2.5 cm of the ground, but Murie (1961) observed evidence of cuttings of willow twigs up to 1.5 m above the ground. Piles are gradually depleted during the winter and may occasionally be raided by snowshoe hares (*Lepus americanus*—Murie 1961). Murie (1961) suggested that individual ownership of haypiles was the norm but some individuals may have as many as 6 piles. Lidicker and Batzil (1999) agreed that individual voles may construct more than 1 haypile. However, they suggested that cooperative construction of haypiles by siblings might occur.

Batzli and Henttonen (1990) reported 2 types of haypiles found in the Toolik Lake region in Alaska: haypiles dominated by herbaceous plants and haypiles dominated by willows. Herbaceous haypiles were placed on rocks and well-drained slopes and contained a variety of palatable herbs (e.g., *Equisetum arvense*, *Epilobium*, *Petasites frigidus*, and *Polemonium acutiflorum*). These piles were often dominated by 1 species, depending on local availability of plants and time of haying. Small amounts of graminoids (*Carex* and *C. canadensis*), aromatic herbs (*Artemesia*), and unpalatable shrubs (*Empetrum nigrum* and *Vaccinium vitis-idaea*) might also be included in the pile.

The willow piles were located slightly off the ground and held in place by the branching base of a 0.5- to 1.0-m-high shrub (Batzli and Henttonen 1993). These piles consisted mostly of the terminal twigs (5–10 cm long) of either *Salix pulchra* or *S. glauca* including several green leaves and often contained large volumes (> 10 l) of material. Examination of the surrounding shrubs showed twig scars up to 1 m above the ground, indicating that voles climbed the shrubs to harvest the twigs. The number of haypiles varied year to year during the study, but not in relation to the number of animals on the grid during the haying season. Whether the total mass of haypiles was related to the density of voles was not determined. Many more haypiles were found within the home ranges of immature *M. miurus* than in the home ranges of adults in 1984 and 1986. This finding suggests that

reproductively active adults may be less involved with haying and that immatures may construct the hay piles cooperatively (Batzli and Henttonen 1993). Many haypiles (79–95%) remained throughout the winter perhaps reflecting the poor survival of immatures in the area.

Perhaps the most vocal of the voles, *M. miurus* makes a high-pitched series of pulsating chirps without modulation, especially when haypiles are being constructed in late summer (Murie 1961; Youngman 1975). Their singing has been described as a metallic "churring sound" and gave raise to their common name—the singing vole. These calls typically given from near a burrow entrance may function for territory defense or warning of predators nearby (Bee and Hall 1956). Youngman (1975) reports calls following an intruding predator as it wandered through the colony of *M. miurus*. Batzli and Henttonen (1990) speculate that because haypiles were often concentrated where clusters of immature animals also occurred, immature siblings may construct haypiles cooperatively. If so, singing may help to coordinate and to defend their collaborative enterprise.

GENETICS

The diploid number (2n) was determined to be 54 chromosomes and the fundamental number (FN) was 72 (Fedyk 1970; Rausch 1964; Rausch and Rausch 1968; Vorontsov and Lyapunova 1986). The X chromosome is large and metacentric (Rausch and Rausch 1968) rather than medium-sized and submetacentric as reported by Rausch (1964). The Y chromosome is small and submetacentric with very short superior arms. Modi et al. (2003) used C-banding and fluorescent in situ hybridization to study the molecular and cytogenic characteristics of repeated DNA sequences and heterochromatin distribution in 9 species of *Microtus* including *M. miurus*. In addition, they provided information regarding chromosomal localization for 6 DNA repeats. Conroy and Cook (2000) reported mitochrondrial cyto-chrome-*b* gene sequence data and Triant and DeWoody (2008) have investigated mitochondrial pseudogenes in *M. miurus*.

Microtus miurus classically has been treated as a member of the subgenus *Stenocranius* (e.g., Hall 1981). However, considerable difference exists in the karyotype of *M. miurus* and *M. gregalis* both in chromosome number (2n = 54 versus 2n = 36) and the number of chromosomal arms (FN = 72 versus FN = 54—Fedyk 1970). Fedyk (1970) concluded that *M. gregalis* is a species cytologically distant and probably reproductively isolated from *M. miurus*.

The karyotypes of *M. miurus* and *M. abbreviatus* agree in number of chromosomes, number of chromosome arms, and the morphology of chromosomal pairs (Fedyk 1970). The sex chromosomes are also morphologically identical. A close sister relationship exists between *M. miurus* and *M. abbreviatus* and is supported by cytochrome-*b* sequences and

chromosomal similarities (Conroy and Cook 2000; Rausch and Rausch 1968). These data probably reflect the relatively recent separation of these 2 species. Rausch and Rausch (1968) reported that a male *M. abbreviatus* bred with a female *M. miurus* produced 2 hybrid fetuses.

CONSERVATION

Microtus miurus is moderately abundant but densities may vary year to year. The species is rated as "Least Concern" on the *Red List of Threatened Species* of the International Union for Conservation of Nature and Natural Resources (2009).

ACKNOWLEDGMENTS

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