

*Clethrionomys gapperi*. By Joseph F. Merritt

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*Clethrionomys gapperi* (Vigors, 1830)

Gapper's Red-backed Vole

- Arvicola gapperi* Vigors, in Gapper, 1830:204. Type locality between York (=Toronto) and Lake Simcoe, Ontario.
- Evotomys carolinensis* Merriam, 1888:460. Type locality Roan Mountain, 6000 ft., Mitchell Co., North Carolina.
- Evotomys galei* Merriam, 1890:23. Type locality Ward, 9500 ft., Boulder Co., Colorado.
- Evotomys occidentalis* Merriam, 1890:25. Type locality Aberdeen, Grays Harbor Co., Washington.
- Evotomys idahoensis* Merriam, 1891a:61. Type locality Sawtooth (Alturas) Lake, 7200 ft., E base Sawtooth Mountains, Blaine Co., Idaho.
- Evotomys fuscodorsalis* J. A. Allen, 1894:103. Type locality Trappers Lake, New Brunswick.
- Evotomys pygmaeus* Rhoads, 1894:284. Type locality mouth of Nisqually River, Pierce Co., Washington.
- Evotomys wrangeli* V. Bailey, 1897:120. Type locality Wrangell, Wrangell Island, Alaska.
- Evotomys ungava* V. Bailey, 1897:136. Type locality NW slope Mt. Ellinor, 4000 ft., Olympic Mountains, Washington.
- Evotomys proteus* Bangs, in Bailey, 1897:137. Type locality Hamilton Inlet, Labrador.
- Evotomys caurinus* V. Bailey, 1898:21. Type locality Lund, east shore of Malaspina Inlet, British Columbia.
- Evotomys phaeus* Swarth, 1911:127. Type locality Marten Arm, Boca de Quadra, Alaska.
- Evotomys limitis* V. Bailey, 1913:133. Type locality Willow Creek, 5800 ft., a branch of the Gilita, Mogollon Mountains, Catron Co., New Mexico.
- Clethrionomys gapperi* Green, 1928:255, first use of name combination.

**CONTEXT AND CONTENT.** Order Rodentia, Superfamily Muroidea, Family Cricetidae, Subfamily Microtinae. The genus *Clethrionomys* comprises about 10 extant species. Some 29 subspecies of *C. gapperi* are recognized (Hall, in press).

**DIAGNOSIS.** Species of *Clethrionomys* are difficult to distinguish morphologically; no single character is sufficient to distinguish *C. gapperi* from other species of *Clethrionomys*. *C. gapperi* differs from *C. rutilus* as follows: tail more slender, and with sparser and less bristly hairs (Hall and Cockrum, 1953); dorsum brighter red; postpalatal bridge generally a solid, truncated shelf (*C. rutilus* has an incomplete palatal shelf or a central notch, Bailey, 1897; Burt, 1946; Hall and Cockrum, 1953; Hall, in press). Bee and Hall (1956) noted much individual variation in shape and ossification of the postpalatal shelf of *C. rutilus* which was influenced by growing season on the Arctic Slope and suggested that the longer growing season of the more southern *C. gapperi* provided sufficient time for development of a well formed palate. Hooper and Hart (1962) reported differences in the urethral processes between *C. gapperi* and *C. rutilus*. The former possessed a single medial finger of the process, the latter a pair of medial processes and a long midventral lobe split distally. Canham and Cameron (1972) found differences between electrophoretic patterns of *C. gapperi* and *C. rutilus*. However, *C. gapperi* has been considered conspecific with the Holarctic species, *C. rutilus* (Bee and Hall, 1956; Youngman, 1975).

*C. gapperi* closely resembles *C. glareolus*, but in the former, the tail is generally shorter, hindfoot longer and enamel of M3 more complex. These characters, in addition to allopatry, justify specific separation (Hinton, 1926). *C. gapperi* and *C. rufocanus* possess acrocentric Y chromosomes, whereas in *C. rutilus* and *C. glareolus* they are metacentric (Hsu and Benirschke, 1970; Rausch and Rausch, 1975); otherwise the chromosomes of all are similar in structure.

**GENERAL CHARACTERS.** Standard external measurements (mm) are: total length, 116 to 172; length of tail, 30 to 50;

hind foot, 16 to 21; length of ear from notch, 12 to 16; weight, 6 to 42 g (Hall, in press). Males and females are similar in size and color. The dorsum has a broad, rusty or reddish band from forehead to rump; band varies from bright chestnut to yellowish brown (occasionally black). The nose and sides of head and body are grayish, washed with pale buff or ochraceous; hairs of venter are black at base and broadly tipped with white, producing a silvery appearance. Tail is bicolored, dark brown to black above, whitish to gray below; feet are pale-drab gray (Fig. 1). Summer pelage is darker and more dusky than winter fur; young animals tend to be darker than adults and usually less ochraceous. Two distinct color phases occur in northern and eastern subspecies: those with dorsal bands of chestnut and those with bands of grayish brown (Jackson, 1961).

Cranial measurements (mm) are: condylobasal length, 20.9 to 25.4; zygomatic breadth, 12.1 to 14.6; interorbital constriction, 3.4 to 4.0; mastoid breadth, 10.4 to 12.0; length of nasals, 6.0 to 8.0; length of maxillary toothrow, 4.7 to 6.1 (Bailey, 1897; Armstrong, 1972). Skull is comparatively weak and rather smooth (Fig. 2), lacking conspicuous ridges; cranium is narrow, smooth and rounded; auditory bullae are well-inflated ventrally and without bony trabeculae; zygomatic arches are slender; incisive foramina are long and parallel-sided; posterior border of palate with or without projection and continuous between alveoli of posterior molars; palate extends back to level of M3 (Miller, 1896; Hooper and Hart, 1962). Shape and size of basiphenooid, ectopterygoid fossae and position of dental foramina were described by Hooper and Hart (1962). Dentition is weak and molars have distinct roots in adults; cheekteeth are small relative to cranial size; enamel pattern of molars with approximate equality of re-entrant angles. Occlusal pattern of molars was described by Hooper and Hart (1962). Dental formula is  $i\ 1/1, c\ 0/0, p\ 0/0, m\ 3/3$ , total 16.

The baculum has a relatively short, broad, basal shaft and three ossified digital processes at the tip. Shaft is flattened dorsoventrally, cup-shaped, and concave on dorsal surface; distally shaft tapers to a blunt tip which supports processes; median digit arched in dorsoventral plane. Measurements (mm) are: length of basal shaft, 1.5 to 2.9; width of base of shaft, 0.40 to 1.5; length of median process, 0.75 to 0.93; width of base of median digit, 0.26 to 0.43 (See Hooper and Hart, 1962 for review of literature).

**DISTRIBUTION.** Gapper's red-backed voles are characteristic of forests of the Hudsonian and Canadian life zones (Fig. 3). In the West, they occur in the Rocky Mountains south to southwestern New Mexico and Arizona. The Columbia River marks their southern limit in the Northwest (Johnson and Osten-



FIGURE 1. Photograph of *Clethrionomys gapperi*, taken in a sub-alpine forest, Boulder Co., Colorado, by J. F. Merritt.

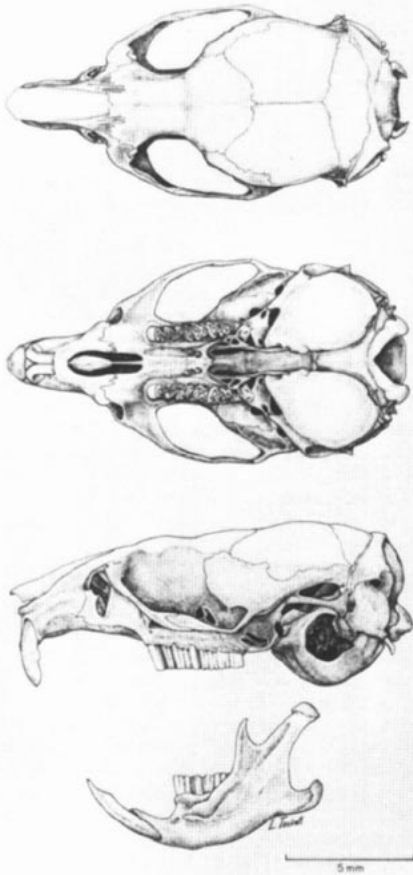


FIGURE 2. Dorsal, ventral, and lateral views of skull, and lateral view of lower jaw of *Clethrionomys gapperi galei*, ODU 171, female, from Boulder Co., Colorado. Drawn by L. Tackett.

son, 1959). Northward in British Columbia and transcontinentally through Canada they display contiguous allopatry with *C. rutilus*. In the East, *C. gapperi* is found in the Appalachian chain south into northern Georgia (Wharton and White, 1967). A third southward extension from Canada into northern Michigan and western North Dakota extends to northern Iowa.

**FOSSIL RECORD.** *C. gapperi* is known from Irvingtonian (Late Kansan) age to Early Recent, as follows: Duck Creek local fauna, north-central Kansas (Zakrzewski and Maxfield, 1971; McMullen, 1978); Little Box Elder Cave, Wyoming (Anderson, 1968); Crankshaft Cave, Brynjulson Caves, and Bat Cave, Missouri (Hawksley et al., 1973; Parmalee and Oesch, 1972; Parmalee et al., 1969); Meyer Cave, southwestern Illinois (Parmalee, 1967); Robinson Cave, Tennessee (Guilday et al., 1969); Natural Chimney's and Clark's Cave, Virginia (Guilday, 1962; Guilday et al., 1977); Hoffman School Cave, Mandy Walters Cave, and Eagle Cave, West Virginia (Guilday and Hamilton, 1973, 1978); Cumberland Cave, Maryland (Van der Meulen, 1978); New Paris Sinkhole No. 4, Pennsylvania (Guilday et al., 1964). Guilday (1971) reviewed the history of the Appalachian mammal fauna including *C. gapperi*. Cave excavations in the Midwest and East were reviewed by Graham (1976), with comments on the importance of Late Wisconsin environmental gradients to the distribution of *C. gapperi*. Macpherson (1965) hypothesized that *C. gapperi* existed in the refugium south of the ice sheet during Pleistocene glaciation and expanded north since that time, coming in contact with *C. rutilus* along the Canadian Arctic tundra. Hoffman and Jones (1970) compared the Late Glacial (13,000 to 10,500 BP) distribution of *C. gapperi* to its present range in the Northern Great Plains.

**FORM.** Three major pelages are juvenile, subadult and adult (Fisher, 1968). Post-juvenile molt begins at about day 33 and is completed from day 90 to 120. In Minnesota, first seasonal molt occurs in fall and results in winter pelage by November;

summer pelage is attained by mid-May (Butsch, 1954). Molting does not occur in pregnant or lactating females.

Phillips and Oxberry (1972) constructed a model of dental evolution in *Microtus* based on comparative histological characters with *C. gapperi*. A mutation (during Early Pleistocene) eliminated formation of the coronal cervix in *Microtus* permitting ever-growing molars. Quay (1953) and Reilly (1956) noted malar-arrangement of cheekteeth of *C. gapperi* that did not prevent their proper function. Perrin (1978) traced calcium deposition in molar root growth of *C. gapperi*; a linear relationship existed between length of the anterior root of M1 and age. Molar roots of *C. gapperi* developed at about day 84. Quay (1954b) examined variations in surface structure and foramina of the bones of the diastemal palate in *Clethrionomys*. Hooper (1968) examined the anatomy of the middle ear and osseous external ear of nine species of microtines. *C. gapperi* has an "open system" resembling that of *Neofiber alleni*. The carotid circulation of *C. gapperi* is similar to that of *Microtus pennsylvanicus* (Guthrie, 1963).

Flank glands were described by Bailey (1897) and Quay (1968). Some *Clethrionomys* show paleness of pelage in the glandular region suggesting a function in visual communication, but histological sections of flank skin revealed no enlarged erector pili muscles (Quay, 1968). Distinct patches may not develop in the first summer; examination ( $n = 194$ ) showed 54% of males and only 9% of females possessed flank glands (Quay, 1968). The meibomian glands of *Clethrionomys*, one of the most primitive microtine genera, are less reduced than those of other voles (Quay, 1954a). The occurrence and relative numbers of sebaceous, apocrine sudoriferous, and mucous glands of the oral lips and angle were described by Quay (1965). Arata (1964) noted that *C. gapperi* possessed the most heavily recurved vesicular glands of the six species of microtines examined.

**FUNCTION.** Foreman (1960) found that *C. gapperi* showed single hemoglobins of identical mobility to those of *Ondatra zibethicus* and *M. pennsylvanicus*. Later, with more advanced techniques, Foreman (1964) found differences between hemoglobins of *C. gapperi* and *M. pennsylvanicus* involving at least 13 peptides. Johnson (1968) analyzed serum proteins and hemoglobins, and indicated that the major hemoglobins of the species of *Clethrionomys* migrate alike. Serum proteins were compared between *C. gapperi* and *C. rutilus* from nine localities in western Canada (Canham and Cameron, 1972). All four transferrins, four of five albumins, and eight of 17  $\alpha$ -globulins occurred only in *C. gapperi*. Mihok (1979a) studied transferrins of red-backed voles from Heart Lake, Northwest Territories; changes in allele frequency correlated with changes in vole density. Maximum velocities of arginase at various temperatures were determined for *C. gapperi* from northern Minnesota and compared to nine other species of mammals from the same location (Boernke, 1977). At 25°C maximum velocity was similar to that of *Blarina brevicauda*, *Peromyscus maniculatus* and *M. pennsylvanicus*. Cricetids exhibited velocities that were higher than values for other homeotherms tested. From analyses based upon hemoglobin concentration, hematocrit ratio, mean corpuscular hemoglobin concentration and oxygen capacity, Sealander (1965) showed that *C. gapperi* has a comparatively high oxygen storage capacity.

McManus (1974), Potter (1975) and Merritt and Merritt (1978a) reviewed energy requirements of *C. gapperi*. Metabolic rates measured at thermoneutrality ranged from about 2.3 to 3.9 cc O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>. Assimilation efficiency was reported as about 78.9% (Johnson and Groepper, 1970; McManus, 1974). Johnson and Groepper (1970) conducted food consumption experiments to determine energy dynamics of *C. gapperi* in the northern Great Plains. The influences of environmental temperature on energy requirements of *C. gapperi* were determined by Opsahl (1959); thermoneutral point was about 26°C and for each degree below 26°C an increase of 0.02 kcal g<sup>-1</sup> day<sup>-1</sup> of energy was required for existence. Daily maintenance requirement was 734 cal g<sup>-1</sup> day<sup>-1</sup>. Buckner and Bergeron (1973) examined energy requirements of *C. gapperi* from southern Manitoba. Oxygen consumption ranged from 4.59 to 6.33 cc g<sup>-1</sup> h<sup>-1</sup>, carbon dioxide production averaged 2.90 to 4.20 cc g<sup>-1</sup> h<sup>-1</sup>, and urinary nitrogen 1.821 to 2.475 mg/h for temperatures of 22.2 to 11.7°C respectively. Active daily metabolism was 6.45 kcal/day for an average 19.1 g vole. Potter (1975) determined an annual energy budget of  $2.91 \times 10^4$  kcal/ha for a *C. gapperi* population from the Hubbard Brook Experimental Forest in New Hampshire. In Colorado, winter collected red-backed voles weighed less and showed lower per gram metabolic rates than the larger summer animals; Merritt and Merritt (1978a) concluded that small size and lowered metabolism reduced food requirements in winter. Several authors have re-

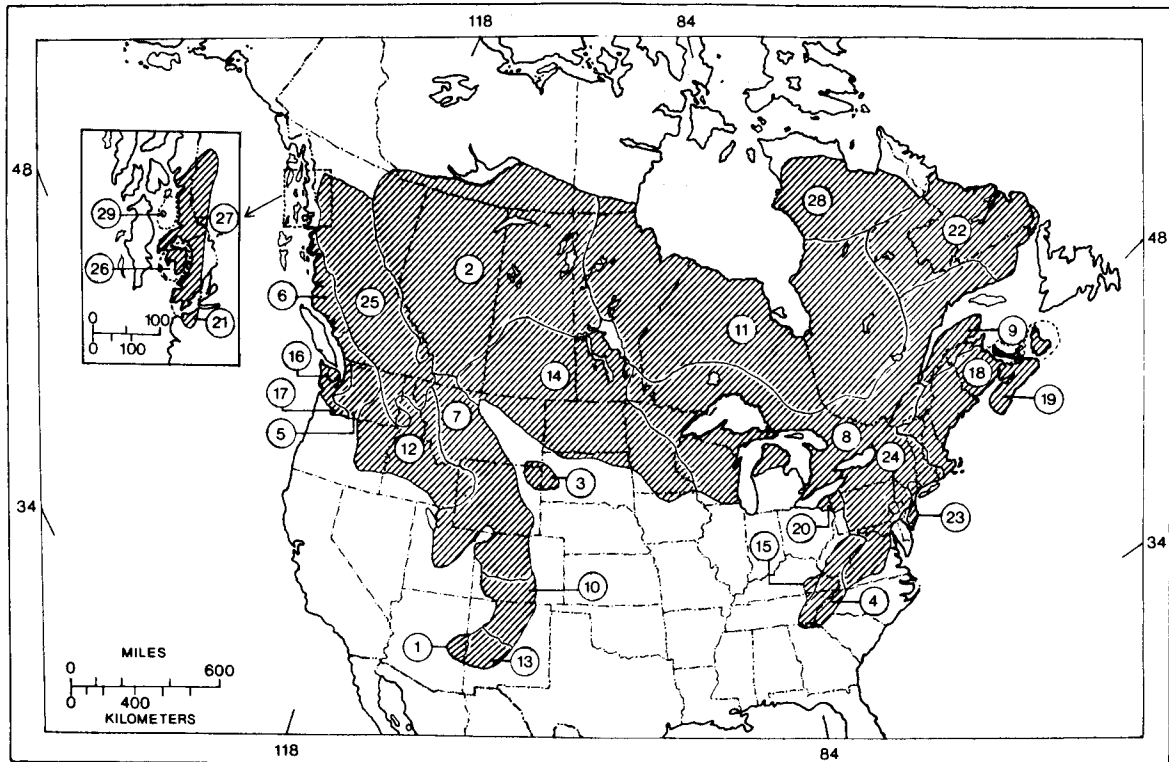


FIGURE 3. Geographic distribution of *Clethrionomys gapperi* in North America. 1, *C. g. arizonensis*; 2, *C. g. athabascae*; 3, *C. g. brevicaudus*; 4, *C. g. carolinensis*; 5, *C. g. cascadenis*; 6, *C. g. caurinus*; 7, *C. g. galei*; 8, *C. g. gapperi*; 9, *C. g. gaspeanus*; 10, *C. g. gauti*; 11, *C. g. hudsonius*; 12, *C. g. idahoensis*; 13, *C. g. limitis*; 14, *C. g. loringi*; 15, *C. g. maurus*; 16, *C. g. nivarius*; 17, *C. g. occidentalis*; 18, *C. g. ochraceus*; 19, *C. g. pallescens*; 20, *C. g. paludicola*; 21, *C. g. phaeus*; 22, *C. g. proteus*; 23, *C. g. rhoadsii*; 24, *C. g. rupicola*; 25, *C. g. saturatus*; 26, *C. g. solus*; 27, *C. g. stikiniensis*; 28, *C. g. ungava*; 29, *C. g. wrangeli*. Modified from Hall (in press).

ported that red-backed voles decrease body weight during autumn and winter and gain weight in spring (See Fuller, 1977b; Merritt and Merritt, 1978a; Perrin, 1979). Body water and fat content of *C. gapperi* were analyzed by Buckner and Bergeron (1972). Water and fat combined made up 76% of the total body weight; little difference was found between sexes. Bergeron (1976) compared the caloric value of *C. gapperi* to that of *P. maniculatus*, *B. brevicauda* and *Sorex cinereus* in Quebec; *C. gapperi* had the lowest caloric value of biomass (1.690 kcal/g). Average thermal gradient in the nasal passage of *C. gapperi* (From tip of nose to cribriform plate, 9.8 mm) was 1.2°C/mm (Schmid, 1976).

Schmid (1972) examined urine osmolality and medullary area of kidneys in *C. gapperi*. Kidney function was correlated with nocturnal activity and changes in ambient vapor pressure and temperatures. Detailed analyses of the water economy of *C. gapperi* were provided by Getz (1962, 1968a, 1968b) and McManus (1974). The high water requirements of *C. gapperi* are well documented; Brower and Cade (1966) reported that red-backed voles drink more than twice as much as predicted on the basis of their weight. *Ad libitum* water consumption ranges from 0.22 to 0.61 cc H<sub>2</sub>O g<sup>-1</sup> h<sup>-1</sup> (See McManus, 1974). Odum (1944) reported an average rate of 22 cc/24 h for an average 27.9 g vole. *C. gapperi* consumed nearly 10 times as much water as *P. leucopus* and *P. maniculatus* from the same location. Getz (1968a) calculated total water budget for *C. gapperi* as 0.46 g g<sup>-1</sup> day<sup>-1</sup>, whereas McManus (1974) determined a higher requirement (0.64 g g<sup>-1</sup> day<sup>-1</sup>). The high water requirement of *C. gapperi* is an important factor in habitat selection.

**REPRODUCTION AND ONTOGENY.** Red-backed voles are polyestrous and exhibit a post-partum heat. Gestation requires from 17 to 19 days. The breeding season lasts about 7 months in the wild, from late winter to late fall (Vaughan, 1969). Year-round breeding occurs in the laboratory (Svihla, 1929). Litter size varies from 2 to 8 (Manville, 1949; Hasler, 1975). Larger litters are from higher latitudes and elevations (Innes, 1978). Age at sexual maturity ranges from 2 to 4 months (Gunderson, 1962;

Svihla, 1929, respectively). Breeding phenology is reported for the following locations: Washington (Svihla, 1931); Colorado (Merritt and Merritt, 1978a); Michigan (Manville, 1949); Minnesota (Butsch, 1954); New York (Fisher, 1968); Northwest Territories (Fuller, 1969); Alberta (Stebbins, 1976); Manitoba (Iverson and Turner, 1976).

Fuller (1969) reported breeding of *C. gapperi* below a mantle of snow near Great Slave Lake, Northwest Territories. In the Front Range of the Rocky Mountains, *C. gapperi* began breeding in late March while 150 to 200 cm of snow covered the ground (Merritt and Merritt, 1978a). Evernden and Fuller (1972) suggested that timing of breeding may be controlled by snow depth. Roth (1974) demonstrated that long-day photoperiod and low temperature stimulated testicular development in *C. gapperi*, whereas Hall (1975) found that termination of breeding is not regulated by cyclic changes in photoperiod.

Postnatal development was detailed by Svihla (1929, 1931), Criddle (1932), Benton (1955) and McCracken (1972). Weight changes during development are from Merritt (unpublished data). At birth, red-backed voles are blind, toothless and hairless except for well-developed vibrissae; color is pink throughout. Measurements at birth (mm) are: crown-rump length, 30; total length, 39; length of tail, 6; length of foot, 6. Weight of newborn ranges from 1.7 to 2.3 g (mean, 1.9). Within 24 h postpartum, the dorsum becomes darkly pigmented due to development of hair, but the venter remains pink. Young are capable of vocalization. Mean weight at day 2 is about 2.9 g. At day 4, young gain partial equilibrium and are able to remain upright most of the time; minute hairs begin to appear on the back, and by day 5 most individuals are able to crawl (average weight, 4.4 g). From day 7 to 8, young are covered with dark gray hair which will gradually assume the characteristic reddish tinge; upper and lower incisors appear, soon to be followed by cheekteeth. Voles may exhibit vocal protests to handling at this time and are able to crawl freely with legs at right angles to body. Mean weight at day 7 is 5.5 g. From day 9 to 11, voles crawl well, scratch themselves with the hindfeet, and in more precocial individuals, eyes may open at this time (mean weight for day 10 is 6.9 g). Eyes of most voles open

from day 12 to 15. The body is covered now by dense, short hair throughout. Young begin to feed on solid food by day 14 and are able to run awkwardly and may climb vertical surfaces; much time is spent grooming (mean weight at day 14 is 8.1 g). Weaning commences from day 12 to 15, and is generally completed by day 17. Weight ranges from 11.5 to 12 g by day 16 to 18. Svihla (1929) indicated that in the one instance when a second litter was born 17 days after the first, the young of the first litter were abruptly weaned. Young of *C. gapperi* may suckle (yet eat solid foods) for at least 3 weeks.

Maximum longevity reported for *C. gapperi* is about 20 months (Manville, 1949), but most voles live about 10 to 12 months in the wild—few survive two winters.

**ECOLOGY.** *C. gapperi* frequents chiefly mesic habitats in coniferous, deciduous, and mixed forests with abundant litter of stumps, rotting logs, and exposed roots. In the West, habitats include forests of ponderosa pine, red and white cedar, hemlock, spruce, Douglas fir, and spruce-fir, grassy meadows, chaparral, willow-grass-sedge, rockslides, and krummholz (Williams, 1955a; Negus and Findley, 1959; Hoffman, 1960; Rickard, 1960; Pattie and Verbeek, 1967; Clark, 1973; Armstrong, 1977). In Canada, *C. gapperi* occupies a wide range of forest habitats, muskegs, sedge marshes, spruce and fir bogs, shrub communities, willow-covered levees, rocky ridges, mesic prairie, and tundra (Morris, 1955; Gabbutt, 1961; Clough, 1964; Fuller, 1969; Pruitt, 1972; Iverson and Turner, 1973; Wrigley, 1969, 1974).

In the Midwest, *C. gapperi* occupies coniferous forests of pine, cedar, spruce, balsam fir, hemlock, and tamarack, deciduous forests of maple, basswood, oak, aspen, and birch, mixed hardwoods, and thick brush (Manville, 1949; Gunderson, 1962; Beer et al., 1954; Iverson et al., 1967). Suitable habitats in eastern United States include forests, cut-over woodlots, forest-edge communities, marsh-grass, stone walls, old fields, and sedge and chelone communities (Miller and Getz, 1972, 1973, 1977b; Kirkland and Griffin, 1974; Richens, 1974).

The influence of fire on the distribution and abundance of *C. gapperi* has been studied in forest and oak-savannas. Compared to other small mammals, *C. gapperi* usually showed a decreased ability to colonize early post-burn communities (see Beck and Vogl, 1972; Martell and Radvanyi, 1977). Given at least two growing seasons, *C. gapperi* may become established in burns as habitat becomes more suitable (i.e. increased food availability and cover) (Ahlgren, 1966). Tester (1965), in contrast, found a greater number of *C. gapperi* following burning of an oak-savanna community. Immigration of adults occurred soon after the burn, thereby increasing density. Clearcutting resulted in an initial increase in abundance of *C. gapperi* in clearcuts adjacent to uncut stands (Kirkland, 1977; Martell and Radvanyi, 1977). Lovejoy (1975) found an increase in density of red-backed voles following logging of dry areas; however, minimal change occurred in numbers after logging of moist sites in a northern hardwood forest of New Hampshire. Powell (1972) noted a higher density of *C. gapperi* where a tornado had blown down trees than in an adjacent standing forest. Population pressure was suggested as a mechanism responsible for the short-term presence of *C. gapperi* in a mine-waste habitat in the Adirondack Mountains (Kirkland, 1976).

Terman (1966) summarized data collected in the "North American Census of Small Mammals" for *C. gapperi*. Population estimates (no./ha) for *C. gapperi* (derived from mark-recapture studies) range as follows: Colorado, 2 to 48 (Merritt and Merritt, 1978a); Minnesota, 0 to 28 (Gunderson, 1962); Michigan, 1.2 to 11 (Manville, 1949); New York, 24 to 65 (Fisher, 1968); Connecticut and Vermont, 0 to 37 (Miller and Getz, 1972, 1977a); New Hampshire, 1 to 7 (Potter, 1975); Northwest Territories, 0 to 54 (Fuller, 1969, 1977a; Mihok, 1979a); Alberta, 0 to 22 (Kucera and Fuller, 1978); Manitoba, 0 to 13 (Iverson and Turner, 1972); New Brunswick, 1 to 4 (Morris, 1955). Density tends to increase during summer, reaching peak numbers in late summer and early fall. A gradual decline in abundance occurs through winter. There seem to be no 3 to 4 year population oscillations in *C. gapperi*. Elliott (1969) indicated that populations in an aspen parkland had no cyclical fluctuations. In New York, Patric (1962) found peak population densities separated by about six years, whereas Grant (1976b) concluded that peaks in abundance occurred at 10-year intervals in Quebec.

Three periods of the year may be critical to survival of *C. gapperi*—autumn freeze, spring thaw and mid-winter conditions (see Fuller et al., 1969; Merritt and Merritt, 1978a; Mihok, 1979b). Predation may act in concert with climatic factors to increase mortality (Kucera and Fuller, 1978).

Data on home ranges were reviewed by Merritt and Merritt (1978b). Means vary from 0.01 to 0.50 ha. In the Rocky Mountains, the average home range under snow was larger than where there was not snow. Buckner (1957) determined the "average cruising radius" to range from 23.2 to 27.2 m in a tamarack and black spruce forest of southeastern Manitoba. In New Hampshire, Potter (1975) found that the "effective trapping area" for *C. gapperi* was 7.6 ha.

Food habits were reviewed by Merritt and Merritt (1978a). Fogel and Trappe (1978) and Maser et al. (1978) provided reviews of the mycophagous habits of *C. gapperi*. Red-backed voles are omnivorous, opportunistic feeders, shifting diet in response to availability of food. Foods eaten by *C. gapperi* include vegetative portions of plants, nuts, seeds, berries, mosses, lichens, ferns, fungi and arthropods (Butsch, 1954; Williams, 1955b; Schloyer, 1977; Perrin, 1979). The hypogeous phycmycete *Endogone* and other fungi are a staple in the summer and fall diet of *C. gapperi*. Insects make up a small part of the diet of the red-backed vole. In Colorado, Merritt and Merritt (1978a) found that during warmer months, *C. gapperi* primarily ate fungi, but shifted to seeds during winter. In New York, the summer diet of *C. gapperi* consisted of nuts, seeds and berries, whereas the major winter food included mostly roots and bark of deciduous trees (Merriam, 1884). Vickery (1979) employed forest feeding stations in a maple-birch-beech association of Quebec to test food preference: small differences were found between *C. gapperi* and *Napeozapus insignis* in the preference for fleshy fruits; activity and consumption increased with increased food density. Analysis of stomach contents of *C. gapperi* following application of Orthene (sprayed to control gypsy moths) indicated that *C. gapperi* consumed many arthropods weakened or killed by insecticide (Stehn et al., 1976).

Few studies have examined the impact of biocides on the demography of *C. gapperi*. Johnson (1976) found no short-term affect of aerial application of polydimethylsiloxane on *C. gapperi* in northern Idaho. In West Virginia, however, Kirkland (1978) noted increased number of *C. gapperi* in a deciduous forest following application of the herbicide 2,4,5-T. Dimond and Sherburne (1969) detected residues of DDT and metabolites in *C. gapperi* following an eradication program for spruce budworm in Maine.

*C. gapperi* was important in the diet of short-tailed weasels in northern Minnesota (Aldous and Manweiler, 1942). In Wisconsin, analysis of 103 scats of the timber wolf yielded only four with remains of *C. gapperi* (Thompson, 1952). Hamilton (1974) reported low numbers of *C. gapperi* in the year-round diet of coyotes from the Adirondack region of New York. Rusch and Doerr (1972) found the red-backed vole an abundant prey item (more frequently eaten than *P. maniculatus* or *M. pennsylvanicus*) in the diet of broad-winged hawks in central Alberta.

Red-backed voles harbor a variety of internal parasites, including protozoans, cestodes, and nematodes. Reviews are provided by Doran (1954a, 1954b, 1955) and Fisher (1968). Additional reports of parenteral parasites were made by Erickson (1938), Dikmans (1940), Freeman and Wright (1960), Kinsella (1967), and Lubinsky et al. (1971).

Ectoparasites comprise fleas, lice, ticks, and mites (Fisher, 1968). About 22 species of fleas infect *C. gapperi*; most are recorded from eastern North America (Fuller, 1943; Benton and Cerwonka, 1960; Gabbutt, 1961; Egoscue, 1966; Kinsella and Pattie, 1967; Miller and Benton, 1973; Benton and Kelly, 1975; Lovejoy and Gaughan, 1975; Timm, 1975). Holland (1958) categorized Siphonaptera infecting *C. gapperi* as "Amphiberingian" and "Western Subarctic" species and commented on distributional patterns. Cook and Beer (1959) and Timm (1975) reported lice infestations. Ticks include *Ixodes angustus* and *Dermacentor andersoni* (Clark et al., 1970; Timm, 1975; Whitaker et al., 1975). Occurrences of mites were reported by Whitaker and Wilson (1974), Timm (1975), Whitaker et al. (1975), and Nutting et al. (1978).

**BEHAVIOR.** The general behavior of *C. gapperi* has been detailed by Mihok (1976, 1979a). Red-backed voles are depicted as rather shy and nervous, commonly exhibiting tooth rattling or chattering when handled (Manville, 1949). He reported that *C. gapperi* periodically underwent a brief shock reaction following ear-punching.

Red-backed voles are promiscuous and generally do not form colonies. However, Criddle (1932) reported that *C. gapperi* formed small colonies during winter. Mihok (1976, 1979a) found male-female encounters were amicable with females dominant; female-female and male-male encounters resulted in avoidance, defensive, and aggressive behavior. Male and female associations

occurred only during estrous. Watts (1970) found that the presence of large adult males inhibited the initial capture of juveniles.

Minor disturbances may result in movement of young from nest, abandonment of young or cannibalism (Svihla, 1929, 1931). Butsch (1954) reported that the male, female, and litter occupied a single nest, but the male moved from the nest as the young grew larger. Males do not care for young, but congeniality exists within the family unit. Studies on activity patterns of *C. gapperi* have centered primarily on northern and eastern subspecies. *C. gapperi* were tested at 60°N and removed southward and tested at 53°N. Voles normally nocturnal in winter and partially nocturnal, crepuscular, and diurnal in summer at 60°N became diurnal for all seasons at 53°N (for review, see Stebbins, 1975). A tendency for greater activity at night than during the day was shown by Baron and Pottier (1977). At Heart Lake, Northwest Territories (60°N), red-backed voles tended to be diurnal in winter, but shifted to primarily a nocturnal and crepuscular rhythm in summer (Herman, 1977). A short (2 to 5 h) activity period each day was noted year-round. In Minnesota, Butsch (1954) found that greatest activity during spring occurred in the early morning, followed by a shift in summer (July) from 2300 to 0300 h. During August, two major activity periods were encountered—from 1900 to 2300 and from 0300 to 0700 h. During fall (October and November), red-backed voles were most active between 1900 and 2300 h. Brown (1971) found activity equal in all periods of the day (0800, 1600, 2400 h) during winter and no apparent marked diel rhythm during snow-free months. Getz (1968c), employing a simulated forest environment, found seven activity periods averaging 2.1 h in duration. Periods of inactivity averaged 1.1 h in length. *C. gapperi* was active throughout the day, but was more nocturnal than diurnal. Getz (1968d) also examined the influence of weather (temperature, humidity, and atmospheric pressure) on the activity pattern of *C. gapperi*. Patterns were regulated primarily by light, and were only slightly modified by changes in temperature and humidity.

Aspects of interspecific competition were reviewed by Grant (1972, 1976a). Field studies have shown that *Microtus pennsylvanicus* may inhibit *C. gapperi* from colonizing grassland habitat during the breeding season (Grant, 1969, 1970a; Iverson and Turner, 1972). In woodland habitat, *M. pennsylvanicus* may be excluded (Cameron, 1964; Morris, 1969; Morris and Grant, 1972; Turner et al., 1975). Grant (1970a) employed an arena (one half grass and the other half maple saplings) to test interaction of *M. pennsylvanicus*, *C. gapperi* and *P. maniculatus*. In response to the two latter species, *M. pennsylvanicus* spent more time in the grassland habitat. Grant (1975) confined *M. pennsylvanicus* and *C. gapperi* to a woodland enclosure. Both species reproduced in the enclosure, but densities were low. Little indication was found of a deleterious interaction between the species. Turner et al. (1975) examined habitat exclusion between *M. pennsylvanicus* and *C. gapperi* in the field and laboratory and concluded that meadow voles and red-backed voles may coexist in the non-breeding season when interspecific aggression is low, but not when interspecific aggression increases with the resumption of breeding in spring. *C. gapperi* and *P. maniculatus* were introduced onto islands off the coast of Maine on which *M. pennsylvanicus* resided (see Crowell and Pimm, 1976). Well-defined habitat preferences existed for each species, and habitat utilization changed with time and with changes in intra- and inter-specific densities. *C. gapperi* displaced both *P. maniculatus* and *M. pennsylvanicus* from woodland habitats—the magnitude of interference increased with an increase in density. Extensive reviews of experimental zoogeography were provided by Grant (1970b, 1976a). Getz (1969) studied behavior of *C. gapperi* and *Peromyscus leucopus* in the laboratory; intraspecific aggression was as frequent as interspecific aggression. Workers examining the ecology of *Napeozapus insignis* have noted a complementary pattern in local distribution between *C. gapperi* and *N. insignis* (e.g., Lovejoy, 1973). *N. insignis* may avoid areas occupied by the more aggressive and intolerant *C. gapperi*. Murie and Dickinson (1973) found that male *C. rutilus* exhibited dominance over *C. gapperi* in enclosure experiments; avoidance was displayed by *C. gapperi* and indifference was exhibited by *C. rutilus* during arena trials between individuals.

Nests of red-backed voles are simple and globular, 75 to 100 mm in diameter, and lined with grass, stems, dead leaves, moss, sphagnum or other litter. *C. gapperi* is reported to use natural cavities, abandoned holes, and nests of other small mammals, which may be marked by many runways and tunnels leading into the site (Criddle, 1932). Gunderson (1976) located a nest elevated on a sphagnum hummock and Jackson (1961) found a nest below

a rotten stump about 45 cm beneath the ground surface. Red-backed voles typically do not construct well-defined runways, but may use those of their microtines such as *Microtus pennsylvanicus* and *Synaptomys cooperi* (Butsch, 1954). However, Jackson (1961) reported a 4.2 m runway that was about 7.5 cm below the ground surface leading to a nest. Caching behavior is reported to occur during autumn (Butsch, 1954).

The usual mode of locomotion is hopping, although running is common under vegetation, logs and debris. *C. gapperi* can jump at least 15 to 20 cm in order to surmount obstructions (Jackson, 1961). *C. gapperi* has been recorded as travelling up to 1.8 m/sec (Layne and Benson, 1954). Red-backed voles are agile climbers, sometimes nesting at a height of 6.1 m (See Getz and Ginsberg, 1968, for review of literature). Red-backed voles swim significantly longer and enter water more readily than do white-footed mice (Getz, 1967).

**GENETICS.** Chromosome studies were reviewed by Rausch and Rausch (1975), and karyograms representing four subspecies of *C. gapperi* were provided by Hsu and Benirschke (1970) and Frechette and Jalal (1971). The diploid number is 56 chromosomes. Species of *Clethrionomys* are distinguishable by the form of the Y chromosome (see DIAGNOSIS). Experimental cross-breeds were attempted by Matthey (1952) with *C. gapperi* and *C. glareolus*, and Zimmerman (1965) with *C. gapperi* and *C. rutilus*; all were unsuccessful. However, Grant (1974) obtained F<sub>1</sub> hybrids from crossing *C. gapperi* and *C. glareolus*, but attempts to produce F<sub>2</sub> progeny were unsuccessful.

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