Water Vole (*Microtus richardsoni*): A Technical Conservation Assessment

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COVER PHOTO CREDIT

Water vole (*Microtus richardsoni*). Photograph by Marion Klaus.

SUMMARY OF KEY COMPONENTS FOR CONSERVATION OF THE WATER VOLE

The water vole (*Microtus richardsoni*) occupies the boreal and alpine zones of major mountain ranges in the northwestern United States and southwestern Canada, extending eastward into the mountains of northern and western Wyoming. In the Rocky Mountain Region (Region 2) of the USDA Forest Service water voles are known only from the Shoshone and Bighorn National Forests. There is a paucity of published studies regarding this species, which hampers effective biological evaluation. In general, water voles are rarely monitored and rather cryptic, and long-term data for estimating population trends across their range are largely absent. Water vole occupancy can be difficult to determine when obvious signs of their use are absent, such as at all locations sampled by Klaus (2003) in the Bighorn National Forest.

If sufficient quality habitat is available, water voles have inherently low biological vulnerability because of their relatively high reproductive potential. During the breeding season females may produce two to three litters of two to ten pups each (Negus and Findley 1959, Brown 1977, Ludwig 1984b, Klaus et al. 1999). Reproductive females occupy the best habitat sites, which have typically been occupied by previous generations of water voles (Ludwig 1981). Water vole populations typically remain low and do not experience the three to four year population cycles common among other *Microtus* species. Occasionally their populations will irrupt, possibly in response to unusually high levels of precipitation during the breeding season (Racey 1960, Klaus et al. 1999). In general, high mortality rates and the harsh alpine and subalpine environment probably prevent regular, cyclical irruptions (Ludwig 1984b).

Water voles have high ecological vulnerability because specific habitat requirements limit their abundance and distribution along a stream, within a watershed, and between adjacent watersheds (Klaus et al. 1999). Water voles occupy short, fragmented reaches of alpine and subalpine streams with narrow channels, about 5º slopes, and stream banks with deep and well-developed soils (Pattie 1967, Ludwig 1981, Reichel 1986, Klaus 2003). In the Bighorn National Forest, water voles are found above 2440 m elevation on streams with Rosgen B or E classification (Rosgen 1994, 1996) and a willow (*Salix*)/wet sedge (*Carex*) riparian vegetation type (Girard et al. 1997, Klaus 2003).

Structural integrity of stream banks is critical for water vole site occupancy, and survival of newborn pups depends upon nest security within the subterranean burrows (Pattie 1967, Ludwig 1981, Klaus 2003). Maintaining stream bank soil structure in which burrows are excavated is therefore essential to nest security and the survival of newborn pups. A matrix population model suggests that the majority of water vole population growth for the breeding season depends upon the survival and reproductive output of the first litter of pups born late June or early July (McDonald and Ise 2002). This early-summer period is also when stream banks are moist and thus most susceptible to compaction. It follows that water voles are likely most sensitive to management decisions that result in impacts to occupied stream reaches during this season. Such decisions could involve the timing and intensity of livestock (e.g., cattle, sheep, horses) use, establishment and improvement of roads and trails and riparian fencing projects.

Rigorous analyses of the impact of specific land uses on water voles are lacking. In a qualitative assessment, Friedlander (1995) concluded that the primary threat to water voles is stream bank degradation due to livestock trampling. Luce (1995) similarly concluded that water voles were precluded from areas by heavy livestock grazing when the vegetative cover of the bank was removed and burrows were trampled. Klaus et al. (1999) and Klaus (2003) found that capture rates were significantly lower along streams grazed by livestock compared to streams not grazed by livestock in both the Shoshone and Bighorn National Forests.

Water vole distribution and abundance are apparently greater on the Shoshone National Forest than on the Bighorn National Forest. On the Beartooth Plateau of the Shoshone National Forest, Klaus (1997) reported capture success rates higher than those reported thirty years earlier in the same location by Pattie (1967). Luce (1995) found water voles present at 71 percent of streams surveyed in the Shoshone National Forest. Water voles are found in most of the riparian areas in the Shoshone National Forest where they would be expected to occur and many locations show visible signs of their presence (Oakleaf personal communication 2002).

In comparison, water voles appear to be rare within the Bighorn National Forest. Capture confirmed water vole occupancy at only 33 percent of the streams where they were expected, and visible signs of their activities, such as runways and latrines, were absent at all sites (Klaus 2003). The lack of captures on the majority of surveyed streams also suggests a rather patchy distribution of water voles in this area, although higher trapping effort may be needed to more confidently conclude that water voles are truly absent from these streams. Unfortunately, no baseline data on water vole populations exist for the Bighorn National Forest, precluding comparisons with historical records. In the Bighorn National Forest, water voles are at the eastern limit of their continental range and are geographically isolated from other water vole populations. The Bighorn National Forest population is probably a remnant of a larger and more contiguous late-Pleistocene population (Brown 1971, Hanski and Gilpin 1997, Beauvais 2000). As with all small and geographically limited populations, the persistence of Big Horn Mountain water voles could be especially sensitive to stochastic events (Soule 1987).

The water vole was listed as a sensitive species in Region 2 of the USDA Forest Service in 1994 (USDA Forest Service 1994). The water vole is not listed as sensitive in other USDA Forest Service regions, nor is it a candidate under the Endangered Species Act administered by the USDI Fish and Wildlife Service. The nonprofit group NatureServe (Arlington, Virginia), along with the network of State Natural Heritage Programs, has ranked the water vole as G5 indicating that the species is demonstrably abundant, widespread, and secure at the continental scale (NatureServe 2001). Hence the species' range-wide geographic vulnerability appears to be low. At a state scale, however, the Wyoming Natural Diversity Database (WYNDD; University of Wyoming, Laramie) has ranked the water vole as S2, indicating a relatively high likelihood of extinction from Wyoming (Keinath et al. 2003). This rank is based on distribution, population trends, and threats for all water voles in the state of Wyoming, including those in Yellowstone and Grand Teton National Parks and USDA Forest Service Region 4 and Region 2.

Importantly, NatureServe and WYNDD maintain a separate status rank for water voles on the Big Horn Mountains: G5T2Q/S1 (Keinath et al. 2003). The "T2Q" indicates possible status as a unique intra-species taxon with a relatively high probability of extinction from its entire continental range, which in this case is the Big Horn Mountains. One phylogenetic study found that water voles from the Bighorn National Forest, currently assigned to *Microtus richardsoni macropus*, are most similar to water voles on the Wasatch Mountains in Utah, currently assigned to *M. r. myllodontus* (Sullivan personal communication 2002). This is of particular interest because both the Wyoming and Utah water voles are ranked as more vulnerable than other water vole populations across their geographic range. If Big Horn Mountain water voles are sufficiently unique from other water voles, managers may need to treat the population as a qualitatively different component of regional biological diversity rather than as a satellite population of a more widespread taxon.

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INTRODUCTION

This assessment is one of many being produced to support the Species Conservation Project for the Rocky Mountain Region (Region 2) of the USDA Forest Service. The water vole (*Microtus richardsoni*) is the focus of an assessment because of its status as a sensitive species in Region 2. Within the National Forest System, a "sensitive species" is a plant or animal whose population viability is identified as a concern by a Regional Forester because of significant current or predicted downward trends in abundance and/or in habitat capability that would reduce its distribution (USDA Forest Service 1994, 1995). Because a sensitive species may require special management, knowledge of its biology and ecology is critical.

This assessment addresses the biology of water voles throughout their range in Region 2, which is restricted to the Shoshone and Bighorn National Forests. Prompt completion of the assessment required establishing some limits on the geographic scope of the literature and data sets reviewed by the authors, and especially on further analyses of existing, but unanalyzed, field data. This was not a major constraint, and in fact did not eliminate much information from the assessment because there is so little known and published about this species. This introduction defines the goal of the assessment, outlines its scope, and describes the process used in its production.

Goal

Species conservation assessments produced as part of the Species Conservation Project are designed to provide forest managers, research biologists, and the public a thorough discussion of the biology, ecology, and conservation status, and management of certain species based on available scientific knowledge. The assessment goals limit the scope of the work to critical summaries of scientific knowledge, to discussion of broad implications of that knowledge, and to outlines of information needs. The assessment does not seek to develop specific management recommendations but rather to provide the ecological background upon which management can be based. However, the assessment necessarily does focus on the consequences of changes in the environment that result from management (i.e., management implications). To our knowledge, management actions specific to water voles or water vole habitat have not been proposed or implemented anywhere within the species' range, so it is not possible to report on the success of deliberate manipulations.

Scope

The water vole species assessment examines the biology, ecology, conservation status, and management of this species with specific reference to the geographic and ecological characteristics of the Rocky Mountain Region (Region 2) of the USDA Forest Service. There is a marked lack of published studies on this species from any geographic area. Therefore, although we have centered this assessment on the few studies from within the region, we have necessarily drawn from studies performed outside the region when appropriate. Also, this document focuses on the reproductive behavior, population dynamics, and other characteristics of water voles in the context of the current environment rather than under historical conditions. The evolutionary environment of the species is considered in conducting the synthesis, but it is placed in a current context. This is illustrated particularly well by our discussions of water voles on the Bighorn National Forest. Global changes in climate and vegetation ca. 10,000 years ago resulted in the isolation of a small population of water voles on the Big Horn Mountains. The current management implications of these events are that Big Horn Mountain water voles probably need to be managed in isolation from adjacent populations, and indeed may need to be treated as a distinct intra-species taxon.

In producing this assessment, we reviewed refereed literature as well as non-refereed publications (particularly Ph.D. dissertations), research reports, data accumulated by resource management agencies, and, to a more limited degree, personal communications and observations. Not all publications on water voles are referenced in the assessment, nor was all material considered equally reliable. The assessment emphasizes refereed literature because this is the accepted standard in science. Non-refereed publications or reports were regarded with greater skepticism and were used primarily when this literature was the only information available for a specific topic. Because few people have studied water voles, and because most studies were conducted over short time periods with relatively few individual water voles, there are significant gaps in the scientific knowledge about this species. Prior to 1976, water voles were mostly known from incidental or museum collections. Typically, only one person has studied any particular aspect of their biology or ecology, and relatively few refereed papers have been published about the species. Most of the information about water voles in Region 2 results from studies done by Pattie (1967) and Klaus (1997, 2003; Klaus et al. 1999, 2001). Some basic information about their biology and ecology

is therefore extrapolated from studies done in other areas of their range and often with other subspecies. Occasionally we have extended basic biological information known for similar species in the same genus to water voles, with appropriate cautions and qualifications. Unpublished data (e.g. Natural Heritage Program records) were important in estimating the current geographic distribution of water voles. These data required special attention because of the diversity of persons and methods used in their collection.

Treatment of Uncertainty

Science represents a rigorous and systematic approach to obtaining knowledge. Competing ideas regarding how the world works are measured against observations. However, because our descriptions of the world are always incomplete and our observations are limited, science focuses on approaches used for dealing with uncertainty. A commonly accepted approach in science is based on a progression of critical experiments to develop strong inference (Platt 1964). However, it is difficult to conduct critical experiments in the ecological sciences, and often observations, inference, good thinking, and models must be relied on to guide the understanding of ecological relations.

In this assessment, the strength of evidence for particular ideas is noted, and alternative explanations are described when appropriate. While well-executed experiments represent a strong approach to developing knowledge, alternative approaches such as modeling, critical assessment of observations, and inference are accepted as sound approaches to understanding features of biology.

Publication of Assessment on the World Wide Web

To facilitate use of species assessments in the Species Conservation Project, assessments are being published on the Region 2 World Wide Web site. Placing the documents on the web makes them available to agency biologists and the public more rapidly than publishing them as reports. More importantly, it facilitates revision of the assessments, which will be accomplished based on guidelines established in Region 2.

Peer Review

Assessments developed for the Species Conservation Project have been peer reviewed prior to release on the web. This report was reviewed through a process administered by the Society for Conservation Biology employing two recognized experts on this or related taxa. Peer review was designed to improve the quality of communication and increase the rigor of the assessment.

MANAGEMENT STATUS AND NATURAL HISTORY

Management Status

In 1994 water voles were specifically designated a USFS Region 2 sensitive species (USDA Forest Service 1994) because the species is uncommon to rare in this region and requires specific riparian habitat that is declining and may be damaged by poor grazing practices (Friedlander 1995) and other management actions. The species has no special listing in other USFS Regions.

The Wyoming Game and Fish Department uses a Native Species Status scoring system of 1 to 4 (1 = most imperiled; 4 = relatively secure) to assess the status of native species in the state. Water voles are assigned a score of NSS3, meaning that populations are generally declining and restricted in distribution, and habitat is somewhat vulnerable to disturbance. As with all native non-game vertebrates, the Wyoming Game and Fish Department requires that field workers receive a collection permit prior to conducting activities that may capture water voles.

The non-profit group NatureServe (Arlington, Virginia) and the network of State Natural Heritage Programs have assigned a global heritage status rank of G5 to the water vole, indicating that the species is common, widespread, abundant, and secure at a range-wide scale. A G5 rank generally indicates the existence of greater than 100 significant centers of occurrence and more than 10,000 individuals of a given taxon (NatureServe 2001). The national heritage status rank for water voles in the United States is N5, indicating they are common, widespread, abundant, and secure at a national scale. State heritage status ranks indicate secure status in most states that support water voles. However, in Wyoming (the only state where water voles occur within Region 2), the water vole state rank is S2, indicating that the taxon is currently imperiled in Wyoming and has a relatively high probability of extinction from the state (Keinath et al. 2003). This rank is based on distribution, population trends, and threats for all water voles in the state of Wyoming, including those in Yellowstone and Grand Teton National Parks, USFS Region 4, and USFS Region 2. Other state rankings

across water vole range in the United States are Idaho (S4, apparently secure), Montana (S4), Oregon (S4), Utah (S3, vulnerable to extirpation or extinction), and Washington (S5, demonstrably widespread, abundant and secure). In Canada water voles are ranked N4N5, meaning the species is apparently secure in that country. In Alberta water voles are ranked S3, and in British Columbia they are ranked S4S5 (NatureServe 2001).

Only two management units in Region 2 support water voles, the Shoshone and Bighorn National Forests. Populations on the Shoshone National Forest are within the main center of occurrence for the species, whereas the water vole populations on the Bighorn National Forest are probably completely isolated to the Big Horn Mountains (**Figure 1**). Because this "island" population probably receives no immigrants or genetic material from other water vole populations, it may be best managed as a stand-alone unit rather than part of an interconnected regional population. The Bighorn National Forest water voles could represent a unique evolutionary trajectory that may extend to subspecific status and be at relatively high risk of extinction from the Big Horn Mountains (Fertig and Beauvais 1999, Keinath et al. 2003). NatureServe and the Wyoming Natural Diversity Database (WYNDD; University of Wyoming) maintain a separate status rank for water voles in the Big Horn Mountains, G5T2Q/S1, because of geographic isolation. The "T2Q" indicates status as a unique intra-species taxon, although the exact degree of taxonomic uniqueness is unknown, with a high probability of extinction from its entire continental range, the Big Horn Mountains. The isolated water vole population in Montana's Big Belt Mountains has not received a separate status rank.

Existing Regulatory Mechanisms, Management Plans, and Conservation Strategies

According to USDA Forest Service (1995), the "Secretary of Agriculture's Policy on Fish and Wildlife Departmental Regulation 9500-4" directs the USDA Forest Service to manage habitats for all existing native and desired nonnative wildlife in order to maintain viable populations. Furthermore, this policy directs the USDA Forest Service to assist states in achieving and setting conservation goals and to evaluate and minimize impacts to species with questionable viability.

Aside from listing the water vole as a sensitive species, no other specific regulatory mechanisms, management plans, or conservation strategies specific to this taxon exist in Region 2. Information collected to date from the Shoshone National Forest indicates that water voles are maintaining adequate abundance and distribution there without any specific management or conservation plan (Pattie 1967, Klaus et al. 1999, Oakleaf personal communication 2002). However, Klaus (2003) reported that water vole populations in the Bighorn National Forest were markedly lower than in the Shoshone National Forest. Because of this difference, and because populations on these forests are not connected, it may be necessary to implement forest-specific, rather than Region-specific, management plans. In general, water voles have high mortality rates among all age classes and usually maintain low population densities. These life history characteristics, the stresses of grazing and drought, and the potential for unique genetic composition due to genetic drift, founder effect, and unique adaptation in the Big Horn Mountains make water voles in the Bighorn National Forest of special management concern.

Biology and Ecology

Few studies over the last 4 decades have focused on *Microtus richardsoni*. Those of Pattie (1967), Anderson et al. (1976), Ludwig (1981) and Klaus (1997) provide the most information. The Ph.D. dissertations written by Pattie (1967), Ludwig (1981) and Klaus (1997), along with the refereed papers written from information contained in these dissertations, provided the major sources of information about water voles for this assessment. Other authors have examined water vole habitat, behavior, and demography, but these investigations have been short-term studies or based on samples of a very few individual water voles. Otherwise, water voles are known from museum records or incidental collections. In this report, information from the Shoshone and Bighorn National Forests of Wyoming within Region 2 is emphasized.

Systematics

Microtus richardsoni, the water vole or Richardson's vole, has a convoluted taxonomic history. Richardson (1829) first described the species as *Arvicola riparius*, which was subsequently revised to *A. richardsoni* in 1942 (see Merriam and Stejneger 1891, Long 1965, Pattie 1967, Ludwig 1984a, Hoffmann and Koeppl 1985, Foresman 2001). Water voles have also been assigned a variety of other names, including *Mynomes*, *Microtus principalis* (Ludwig 1984a), and *Aulacomys* (Rhoads 1894, Carleton 1985).

While the relationship between *Microtus richardsoni* and the Old World water vole, *Arvicola*
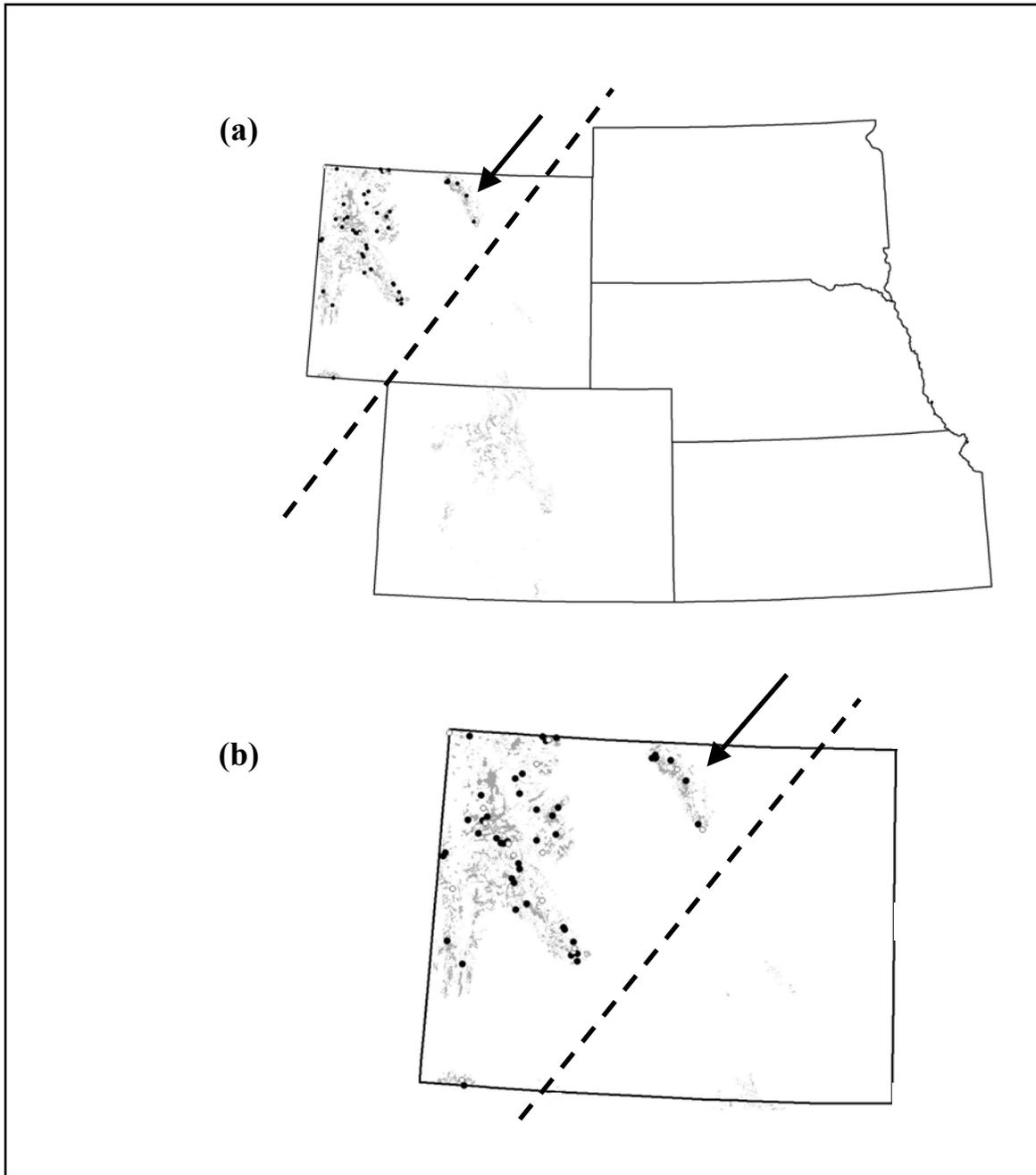
Figure 1. Predictive range map for the water vole (*Microtus richardsoni*) in (a) all states within USDA Forest Service Region 2 and (b) the state of Wyoming. Gray shading shows ecological systems that encompass land cover types associated with water voles and that fall within the biophysical envelope suitable for water voles. Solid dots are points of known water vole occurrence used to model the biophysical envelope; open dots are points of known occurrence withheld from the modeling process and used for independent validation. Dashed line indicates the generally-accepted eastern boundary of water voles in this region. Note that water voles on the Big Horn Mountains (arrow) are predicted to be completely isolated from other populations to the west. From Beauvais et al. (2003).

terrestris, has been unclear, the New World water voles have been placed in the genus *Microtus* rather than *Arvicola* for several reasons, including specific characteristics of dentition, flank glands (Burns 1982), stomach anatomy (Carleton 1981), and mitochondrial DNA (Conroy and Cook 2000). The *Microtus* and *Arvicola* genera appear to be separated by about 1.5 x 10^6 years (Repenning 1980).

Microtus richardsoni has the primitive number of chromosomes for *Microtus* (Jannett and Jannett 1974) and may be an early variant of *Microtus* that evolved from a Siberian *Mimomys* (Ludwig 1984a). A clade consisting of *Microtus californicus*, *M. longicaudus*, and *M. richardsoni* was proposed by Modi (1987) based on chromosomal banding patterns, but mtDNA restriction analysis did not support this grouping (Debry 1989). Debry (1989) proposed that the ancestors of a *M. townsendii—M. oregoni—M. richardsoni* clade was in the Pacific taiga at least 500,000 years ago, and *M. richardsoni* became isolated in refugia of the Rocky Mountains during the Wisconsin glacial. Conroy and Cook (2000) unexpectedly found that *M. richardsoni* appeared to be a sister species to *M. pinetorum*.

Few water vole fossils have been found. *Microtus richardsoni* fossils from Alberta, Canada, predate the Late Pleistocene glacial maximum at about 18,000 years BP (Burns 1982). Water vole fossils have also been found at Warm Springs, Montana (Zakrzewski 1985) and in Wyoming (Ludwig 1984a).

Despite a number of studies based on morphology and molecular markers, change and uncertainty has characterized the classification of New World water voles. One systematic classification of *Microtus richardsoni* is outlined below (Burns 1982, Ludwig 1984a, Anderson 1985, Carleton 1985, Zakrzewski 1985).

> Class Mammalia, Linneaus 1758; Subclass Theria, Parker and Haswell 1897;
> Infraclass Eutheria, Gill 1872; Order Rodentia, Bowdich 1821;
> Suborder Myomorpha, Brandt 1855; Superfamily Muroidea, Miller and Gidley 1918;
> Family Muridae, Gray 1821; Subfamily Arvicolinae, Gray 1821;
> Genus *Microtus*, Bailey 1900 (Schrank 1795); Subgenus *Aulacomys*, Rhoads 1894;
> Species *richardsoni*, DeKay 1842.

Four subspecies of *Microtus richardsoni* are currently recognized: *M. r. arvicoloides*, *M. r. macropus*, *M. r. myllodontus*, and *M. r. richardsoni*. Only *M. r. macropus* is known to occur within Region 2 (Long 1965, Hall 1981, Hoffmann and Koeppl 1985, Ludwig 1984a, 1999). *Microtus richardsoni macropus* type specimens come from 2,835 m in the Pahsimeroi Mountains, Custer County, Idaho (Long 1965).

Microtus richardsoni myllodontus, the subspecies of water vole found in Utah, is only weakly differentiated from *M .r. macropus* (Long 1965). Long (1965) observed that *M. r. myllodontus* had larger auditory bullae, less irregularity in the infraorbital foramina, and a mandible strongly inset at the third molar. These comparisons were made with specimens from Uinta County, Wyoming and the holotype of *M. r. macropus*. Comparisons were not made between the Utah water voles and those found in the more distant Big Horn Mountains. These two populations clustered together in a phylogenetic analysis of mtDNA (Sullivan personal communication 2002); more study is needed to clarify the relationship between these two groups.

Post-Pleistocene isolation of boreo-alpine environments along the Rocky Mountains accounts for much of the speciation and subspeciation found in mammals within this region because of the combined forces of founder effect, genetic drift, and possibly adaptation (Long 1965, Lindsay 1987, Beauvais 2000). For the past 8,000 to 10,000 years, dry basins dominated by shrubs and grasses have surrounded the Big Horn Mountains. As a consequence of this isolation, a number of relict mammal populations are known to have developed into unique subspecies in the Big Horn Mountains: montane vole (*Microtus montanus zygomaticus*; Jannett 1999), American pika (*Ochotona princeps obscura*; Hafner and Sullivan 1995, Smith 1999), least chipmunk (*Tamias minimus confinis*; Bergstrom 1999), and snowshoe hare (*Lepus americanus seclusus*; Murray 1999) (see also: Long 1965, Hall 1981, Clark and Stromberg 1987, Beauvais 1997, Beauvais 2000). Based on these subspeciations, and on similar patterns of subspeciation in boreo-alpine mammals on the nearby and similarly isolated Black Hills (Long 1965, Turner 1974, Hall 1981, Clark and Stromberg 1987, Lindsay 1987, Hafner et al. 1999, Merritt 1999, Young 1999), several other species including American marten (*Martes americana*), red squirrel (*Tamiasciurus hudsonicus*), southern red-backed vole (*Clethrionomys gapperi*), and water vole may be represented by unique and heretofore undescribed subspecies on the Big Horn

Mountains. Because genetically distinct populations are important components of biotic diversity, and because such populations may receive special protections, it is important to determine if water voles in the Big Horn Mountains are a unique subspecies. This issue demands more study.

General species description

Water vole pelage is dense, without stiff hairs, and gray to dark sepia or dark reddish brown, often with black-tipped hairs (Hall and Cockrum 1953; **Figure 2** and **Figure 3**). Ventrally, they are white, silver or gray. The tail may or may not be distinctly bicolored. When bicolored, it is brown above and gray to white underneath (Hall and Cockrum 1953). In comparison to other voles, water voles have a thick, wooly undercoat with long guard hairs (Carleton 1981). The soles of their feet are not densely haired (Glass 1981), and ears and eyes are small (Foresman 2001).

Water voles have a blunt muzzle, a sturdy skull and rostrum, well-developed zygomatic arches, and small, flattened tympanic bullae (Long 1965, Ludwig 1984a, Carleton 1985). Their dental formula is i1/1, c0/0, p0/0, m3/3 (Ludwig 1984a). They have a total of 16 prismatic, unrooted teeth (Ludwig 1984a) and a longer upper molar row than other arvicolines (Long 1965). Water voles have proodont incisors and the nasopalatine apertures are posterior, whereas most *Microtus* have orthodont or opisthodont upper incisors and the nasopalatine apertures are intermediate in position (Carleton 1981). The first molar has five closed triangles while the second molar has an anterior pair of triangles that are usually confluent. The third molar has two or three closed triangles with three transverse loops (Hall and Cockrum 1953) and only two deep reentrant angles on the inner side (Glass 1981). Long (1965) reports irregularly shaped infraorbital foramina and offset tooth-rows in most specimens of water voles. Glass (1981) observed that the incisors protrude far beyond the premaxillae.

The skulls of *Microtus richardsoni* can readily be distinguished from those of other *Microtus* species that occur within their range. *Microtus pennsylvaticus* has a 5th closed posterior loop on the second upper molar, and both *M. montanus* and *M. longicaudus* have larger auditory bullae (Long 1965, Foresman 2001).

Field identification of over-wintered, adult water voles is based upon their large size, weight, and hind foot length (**Figure 2** and **Figure 3**). Morphological measurements important for field identification are provided in **Table 1**. Males are generally larger than females. Unlike adults, juveniles can easily be confused with other *Microtus* (particularly *M. montanus*, *M. longicaudus*, and *M. pennsylvanicus*), but the hind feet of juvenile water voles are generally larger than those of adults of sympatric species. One 18 g juvenile

Figure 2. Adult water vole (*Microtus richardsoni*) in the Shoshone National Forest, Wyoming. Photograph by M. Klaus.

Figure 3. Adult water vole (*Microtus richardsoni*) in the Bighorn National Forest, Wyoming. Photograph by M. Klaus.

Table 1. Published body dimensions of adult water voles (*Microtus richardsoni*). Values indicate ranges unless otherwise noted.

Source	Total length (mm)	Tail length (mm)	Hindfoot length (mm)	Ear length (mm)	Weight (g)
Hall and Cockrum (1953)	198 - 261	69 - 92	25 - 30	15 - 20	112 - 123.3 (mean 118)
Long (1965)	220 - 240 (mean 228)	70 - 76 (mean 73)	26 - 29 (mean 26.8)		
Ludwig (1984a)	198 - 274	66 - 98	25 - 34	15 - 20	
Ludwig (1984a); overwintered males					72 - 150 (mean 113.7, SE 1.7)
Ludwig (1984a); overwintered females					68 - 140 (mean 98.9, SE 1.3)
Clark and Stromberg (1987)	212 - 260	70 - 85	25 - 30	15 - 20	85 - 120
Ludwig (1999)	234 - 274 (mean 252)	66 - 98			72 - 150 (males) 68 - 140 (females)
Streubel (1999)	198 - 224	66 - 98	25 - 34	15 - 20	120
Foresman (2001); males	238.5	76.4	25.9	16.9	112.7
Foresman (2001); females	219.3	72.6	25.8	15.0	100.0

water vole had a hind foot measurement of 23.5 mm (Klaus 1997), while the hind foot length of adult *M. montanus*, the most common sympatric species in Region 2, ranges between 17 and 21 mm (Clark and Stromberg 1987). Length of the hind foot is a reliable characteristic for field identification of juvenile water voles (Ludwig 1984a, Klaus et al. 1999). The number of plantar tubercules on the hind foot has been used to identify Arvicolidae species in the past (Carleton 1985), but confusing results (e.g., Hollister 1912, Hall and Cockrum 1953, Glass 1981, Klaus 1997) indicate that this is an unreliable characteristic for field identification of water voles.

Distribution

Ancestors of the *Microtus* dispersed into the Nearctic across the Bering land bridge and first appeared in the New World in the early Pleistocene (Repenning 1980, Zakrzewski 1985). The genus quickly diversified into 65 different species (Conroy and Cook 2000). Following Pleistocene glaciations, water voles probably followed tundra-like vegetation into high elevations and became isolated in refugia there (Hoffmann and Koeppl 1985).

The current global range of water voles is shown in **Figure 4**. In the western United States, water voles are found between 914 and 3,201 m in elevation (Hall 1981, Ludwig 1981) while in Canada they range between 1,524 and 2,378 m (Banfield 1974, Ludwig 1981). Water voles are found in two separate alpine and subalpine regions, one on the west coast (Oregonian province, Hudsonian Zone) and one in the Rocky Mountains (Rocky Mountain montane taiga, Montanian and Coloradan provinces) (Ludwig 1984a, Hoffmann and Koeppl 1985; **Figure 4**). These two areas are separated by the dry ecosystems of the northern Great Basin and lower interior Columbia Basin, which are probably broad-scale barriers to water vole dispersal. On the west coast, *Microtus richardsoni arvicoloides* is found in the Cascade Mountains of Washington and Oregon and in the Coast Mountains of British Columbia (Ludwig 1984a). In the Rocky Mountains, *M. r. richardsoni* is found in central Alberta; *M. r. macropus* is found in eastern Oregon, central and northern Idaho, Montana, and Wyoming; and *M. r. myllodontus* is found in southern Idaho and Utah (Hall 1981, Ludwig 1984a, Hoffmann and Koeppl 1985). Phylogenetic sequencing analysis suggests that water voles dispersed from the Rocky Mountains to the Cascade Mountains (Sullivan personal communication 2002). More information is needed to understand the relationship between water voles in these two regions.

In Region 2, water voles (assumed to be *Microtus richardsoni macropus* only) are known only from the Bighorn and Shoshone National Forests (**Figure 1** and **Figure 4**). Water voles have been documented in the Big Horn River, Little Big Horn River, Upper Tongue River, Middle Fork Powder River, and Crazy Woman Creek watersheds of the Bighorn National Forest. Water voles have been documented in the Upper Yellowstone River, Clark's Fork River, North Fork Shoshone River, South Fork Shoshone River, Greybull River, Upper Wind River, Popo Agie River, and Sweetwater River watersheds of the Shoshone National Forest (**Figure 1** and **Figure 4**). Presence in the remaining watersheds of both management units is suspected but as yet unproven via capture or observation.

Water voles have been captured as low as 2,484 m in the Big Horn Mountains and as high as 3,188 m in the Beartooth Mountains. They have not been captured below 2,440 m in Region 2 (Klaus et al. 1999, Klaus 2003). Although regional distribution maps (e.g., Hall 1981, Ludwig 1999) imply contiguous water vole occupation between the Beartooth/Absaroka mountains and the Big Horn Mountains, the intervening Big Horn Basin is probably too dry and warm to support them. This basin is the driest and warmest portion of Wyoming, with uplands dominated by sagebrush steppe and cold desert scrub. Water voles have not been documented from riparian areas in the Big Horn Basin, nor are they known from similar habitats elsewhere in their range.

A spatial extrapolation of the environmental conditions at points of known water vole occurrence clearly excluded the Big Horn Basin as an area of potential habitat (**Figure 1**). Details of this mapping effort are in Beauvais et al. (2003). Briefly, the analysis was accomplished by first plotting all points of water vole occurrence in Wyoming in the multivariate space defined by five predictor variables: elevation, mean annual precipitation, mean number of annual frost days, mean minimum January temperature, and mean maximum July temperature. The 5-dimensional volume encompassed by these points was described statistically to set it apart from the rest of the state. This "biophysical envelope" was then mapped, and subsequently clipped with a spatial layer of all land cover types associated with water voles, as identified by the Wyoming Gap Analysis Project (Merrill et al. 1996). This mapping procedure is under review and may be revised in the future to produce more accurate and applicable maps of water vole distribution.
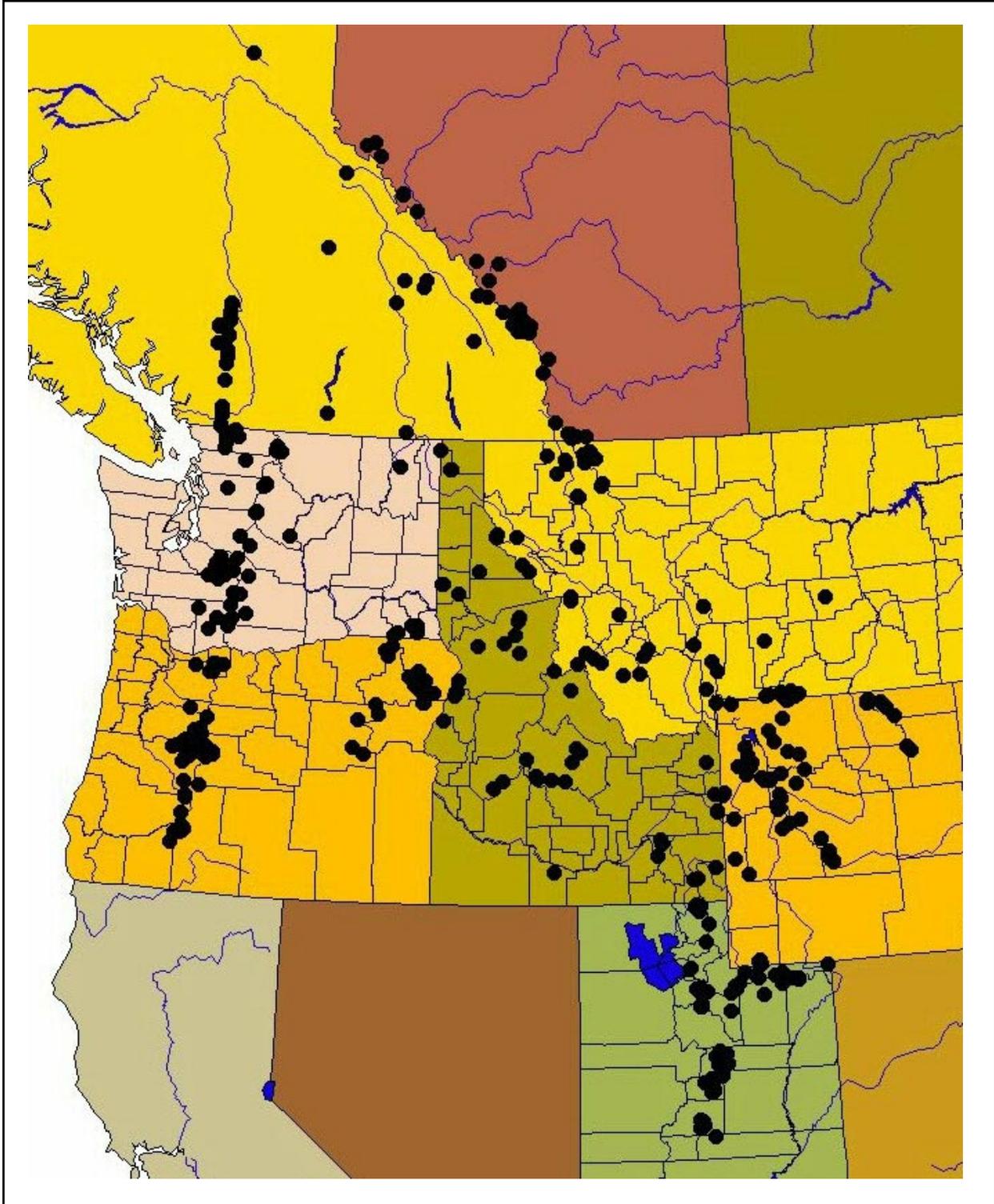
Figure 4. Locations (black dots) where water voles (*Microtus richardsoni*) have been captured or observed throughout their global range. Data was compiled and mapped by the Wyoming Natural Diversity Database (University of Wyoming, Laramie) in summer 2002. Contributing sources for point locations are Carlson (2002), Dark-Smiley (2002), Johnson and Cassidy (1997), Long (2002), Ludwig (2002), Nagorsen (2002), Nordstrom (2002), Oliver (2002), Patton (2002), Slade (2002), Stephens (2002), and Verts and Carraway (1998).

Isolation

Water vole populations in the Big Belt Mountains, Montana, and the Big Horn Mountains, Wyoming, are probably true relicts that are completely isolated from other populations by dry, warm, low elevation basins (Hoffmann and Jones 1970; **Figure 1**). In general, colonization of island mountain ranges by montane mammals occurs very infrequently in western North America (Brown 1971). *Microtus richardsoni* Pleistocene fossils are missing in the Utah portions of the Great Basin, indicating that low elevations here are barriers to dispersal for a high elevation specialist (Rickart 2001). On a regional scale, the boreal habitats of western Wyoming and Utah are separated from similar habitat found in southeastern Wyoming and Colorado by the xeric Wyoming Basin and Green River Canyon region (Findley and Anderson 1956). Water voles occur only in areas to the north and west of the Wyoming Basin and are not known from the Southern Rocky Mountains in Wyoming or Colorado (Findley and Anderson 1956, Fitzgerald et al. 1994).

In the Shoshone and Bighorn National Forests, the regional and local distribution of water voles is highly discontinuous (Klaus et al. 1999, Klaus 2003). Within the Shoshone National Forest, insignificant genetic distances were found between water voles in four adjacent watersheds, suggesting gene flow between adjacent basins. However, significant genetic distances were found between water voles in the Beartooth Mountains and those from Togwotee Pass 150 miles to the south in the Absaroka Mountains (Klaus et al. 2001); this is discussed in more detail in the demography section. The pattern of relatedness between adjacent, but not distant, watersheds is assumed to hold for water voles in the Bighorn National Forest as well, but there are no specific data for this area.

Abundance

Water voles are uncommon throughout their range. In a six year study in the Cascade Mountains of Oregon, water voles constituted only 1 percent of the 4,500 individual small mammals captured (Hooven 1973). In a two year survey of small mammals on the Bighorn National Forest, Beauvais (1997) captured over 1,000 individuals of 13 species but failed to capture any water voles. Both of these studies employed techniques that are effective at capturing water voles. However, although both studies sampled some water vole habitat, neither was specifically focused on capturing water voles or producing complete inventories of riparian habitat. Nevertheless, the lack of captures relative to other species indicates a general rarity of water voles in the small mammal communities of the Cascade and Rocky Mountains. Water voles are typically found in small populations of 8 to 40 animals beside alpine and subalpine streams (Hollister 1912, Racey and Cowan 1935, Pattie 1967, Hooven 1973, Anderson et al. 1976, Ludwig 1984a, 1988, Clark and Stromberg 1987, Klaus et al. 1999).

Within Region 2, water voles were less abundant in the Bighorn National Forest than in the Shoshone National Forest (Klaus et al. 1999, Klaus 2003). During a five year study in the Bighorn National Forest, 55 water voles (18 adults and 37 juveniles) were captured during >4,000 trap-intervals along 14 of 21 streams that met their general habitat criteria. The highest relative abundance (3.8 individuals/100 trap-intervals) was recorded at the Rooster Hill exclosure, where five water voles were captured during 130 trap-intervals along 88 m of suitable streamside habitat (Klaus 2003).

In contrast, during a three year study in the Beartooth Mountains of the Shoshone National Forest, 196 water voles (91 adults and 105 juveniles) were captured during > 5,000 trap-nights along all 10 streams sampled. The highest relative abundance (11 individuals/100 trap-nights) was recorded below Frozen Lake, where 14 water voles were captured during 125 trap-nights along 1,400 m of suitable streamside habitat (Klaus et al. 1999).

In the front ranges of southern Alberta, Anderson et al. (1976) noted that each location in their study showed visible signs of water vole activity, such as runway systems and burrow entrances. Signs of water vole activity, such as runways (**Figure 5**), burrows (**Figure 6**), and latrines (**Figure 7**), were obvious along the streams in the Shoshone National Forest but rare on the Bighorn National Forest. In the Bighorn National Forest, signs were present but difficult to observe and the only way to determine water vole site occupancy was to capture them (Klaus 2003). Presumably, water vole population levels are too low in the Bighorn National Forest for visible signs of their occupancy to develop on the landscape.

Population fluctuations

While many voles are well known for their three to four year population cycles (Taitt and Krebs 1985), regular periodicity has not been observed among water voles. Lack of periodicity may be due to the dampening effects of the severe alpine climate (Ludwig 1984a), high mortality rates (Ludwig 1984a), or variable

Figure 5. Water vole (*Microtus richardsoni*) runway at Wyoming Creek, 3188 m elevation, Shoshone National Forest, Wyoming. These runways are signs of water vole presence and were commonly observed on the Shoshone National Forest, but rarely observed on the Bighorn National Forest. Photograph by M. Klaus.

precipitation levels (Klaus et al. 1999). Racey (1960) encountered high densities of water voles at Alta Lake in the Pemberton Valley in British Columbia during the summers of 1927, 1949, and 1958. During each of these years, precipitation was higher than average (Simpson et al. 1932, Strauss and Reichelderfer 1959, Connor and White 1965). In the Shoshone National Forest, the summer reproductive seasons of 1990 and 1991 were drier than the 30 year mean, but the reproductive season of 1992 had almost double the precipitation of the 30 year mean. Relative to 1990 and 1991, in 1992 more embryos were found in trap-killed females ($t = 2.67$, $df = 5$, $P < 0.05$), more juvenile males showed signs of reproductive activity ($t = 2.49$, $df = 6$, $P < 0.05$), capture success was greater ($U = 100.5$, $P < 0.04$), and higher population densities (15.14 voles/1000 m of stream in 1992; 11.55 voles/1000m of stream averaged across 1990 and 1991) were recorded (Klaus et al. 1999).

Figure 6. Water-level burrow entrance used by released water voles (*Microtus richardsoni*) at Bald Mountain Creek, 2743 m elevation, Bighorn National Forest, Wyoming. Photograph by M. Klaus.

Klaus et al. (1999) interpreted the positive relationship between precipitation and water vole density as resulting from a combination of increased availability of suitable habitat (in the form of formerly dry streambeds and side channels) and increased reproductive output per individual female (more females occupying sites that support reproduction and more pups per litter). Hence, the low abundance generally reported for water voles in Region 2 may not be solely a consequence of the difficulties in capturing them or limited sampling effort in suitable streamside habitat. It may reflect a chronically low population density and restricted distribution in response to generally low precipitation.

However, it is possible that other factors are responsible for the positive relationship between precipitation and water vole density. For example, it may be that water voles are more trappable in wet years because streamside habitat is flooded and voles are concentrated in smaller areas. Further research into the relationship between precipitation and water vole demographics is needed, because this is an issue of potentially great management importance.

Heavy grazing of water vole habitat by large mammals is another factor that may inhibit population cycles. Douglass and Frisinna (1993) found that grazing cattle reduced plant cover and increased the vulnerability of *Microtus montanus* to predation. In this situation, local population densities remained consistently low. Clearly, there are several aspects of large mammal grazing (e.g., seasonal timing, duration, intensity, species of grazer) that could play a role in suppressing small mammal populations; currently there is no published research that documents the specific effects of these factors on water voles.

Long-term population trends

Studies of long-term density changes are absent from the literature, but according to Clark and Stromberg (1987), "water voles were frequently collected in Wyoming through the 1940's. Since the 1960's, we are aware of only three specimens taken in a very small meadow of the Grass Creek drainage. Improper grazing of federally managed lands is particularly harmful to this vole because the wet montane meadows are

Figure 7. Water vole (*Microtus richardsoni*) latrine in the soft mud beside Wyoming Creek, 3188 m elevation, Shoshone National Forest, Wyoming. These latrines are signs of water vole presence and were commonly observed on the Shoshone National Forest, but were not seen on the Bighorn National Forest. Photograph by M. Klaus.

often overgrazed when cattle congregate around water sources." A more recent review of capture data presents a different picture. The WYNDD database documents 79 locations where water voles have been captured in Wyoming; 40 were documented prior to 1973, and the remaining 39 were documented after 1991. It is obviously difficult to draw solid conclusions regarding population trends from these kinds of data without a thorough understanding of the intensity and distribution of sampling effort.

In the Bighorn National Forest 55 water voles were captured between 1997 and 2001 (Klaus 2003), and in the Shoshone National Forest 196 water voles were captured between 1990 and 1992 (Klaus et al. 1999). In 1957 water voles were captured at Crumarine

Creek, Latah County, Idaho, but recent attempts to capture water voles at this site were unsuccessful. This area has been impacted with traffic, recreation, logging pressure, and may have been grazed in the past (Demboski personal communication 2001). Unfortunately, long-term water vole population trends have not been monitored and there are few data with which to test hypotheses regarding the impacts of land use on population size.

Along a creek east of Beartooth Pass (**Figure 8**), Klaus (1997) reported population densities of water voles (average 13.3 water voles/1000 m streamside habitat; approximately 3.3 water voles/ha) higher than those reported 30 years earlier by Pattie (1967; average 0.6 water voles/ha), suggesting at least population stability if not increase over the past 30 years. Livestock do not graze this area, nor is it frequently used for recreation. In three seasons of trapping at this location, Klaus (1997) encountered only one other person in the area. Baseline population data do not exist for water voles in the Bighorn National Forest.

Seasonal population trends

Water vole populations typically reach a seasonal peak in August or September, increasing 0.8 to 6.2 times the initial population size in April or May (Ludwig 1988). August or September water vole densities (water voles/ha) of 17.6 to 32.5 (Anderson et al. 1976), 0.2 to 12.2 (Ludwig 1981) and 0.2 to 1.0 (Pattie 1967) have been reported. Statistical measures of precision for these density estimates were not reported. Klaus et al. (1999) estimated mean ecological densities (water voles/1000 m streamside habitat) of 11.5 during dry summers, 15.1 during an exceptionally wet summer, 9.0 in drainages grazed by both cattle and sheep, and 13.8 in ungrazed drainages in the Shoshone National Forest. In the Bighorn National Forest, estimated ecological densities (water voles/1000 m streamside habitat) ranged from 3 to 24 in grazed drainages and from 15 to 57 in ungrazed drainages (Klaus 2003).

Water vole populations occasionally irrupt when precipitation increases, as documented by Klaus et al.

Figure 8. Occupied water vole (*Microtus richardsoni*) habitat at Beartooth Pass, 3140 m elevation, Shoshone National Forest, Wyoming. Soil is well developed and banks overhang the stream to such an extent that the water is hidden from view. During the 1992 reproductive season precipitation was almost double that of the 30 year mean, and water vole captures more than tripled relative to the drier seasons of 1990 and 1991 (Klaus et al. 1999). During 1990 and 1991, water vole abundance at this site was similar to that reported by Pattie (1967). Photograph by M. Klaus.

(1999) and described anecdotally by Racey (1960). These irruptions likely result from the combined effects of increased availability of suitable habitat, larger seasonal populations, and increased reproductive output of individual females. With high precipitation, runways (**Figure 5**), burrows (**Figure 6**), and latrines (**Figure 7**) were observed in the Shoshone National Forest along small, ephemeral creeks and side drainages that were not occupied in previous years (Klaus et al. 1999). Adult female water voles maintain exclusive home ranges, and more adult females can be supported in a given area when side drainages become suitable (Ludwig 1981, 1984a). More embryos per female and increased reproductive activity in juvenile males were also observed when precipitation increased (Klaus et al. 1999).

Circadian activity patterns

Water voles are semi-aquatic, primarily nocturnal, colonial, active year-around, and regularly use nests built on the ground surface, belowground, and beneath snow (Racey and Cowan 1935, Anderson et al. 1976, Ludwig 1981, 1984a, Burns 1982, Klaus et al. 1999). Hollister (1912) reported that water voles were caught only at night, despite carefully set, undisturbed daytime trapping efforts. In contrast, Bailey (1936), Dalquest (1948), and Ludwig (1981) asserted that water voles are often active during the day. In the Shoshone National Forest, but not the Bighorn National Forest, water voles were observed during the day along runways or in streams, but the vast majority of captures in both the Shoshone and Bighorn National Forests occurred at night (M. Klaus, unpublished data). No daytime activity was observed in the Bighorn National Forest, except for released animals.

Daily activity patterns

Water voles usually clear and maintain surface runways 5 to 7 cm wide through grasses, forbs, sedges (*Carex*), willows (*Salix*), and mosses (Ludwig 1984a; **Figure 5**). Runways were commonly observed in the Shoshone National Forest, but not in the Bighorn National Forest. Streams are incorporated into water vole activity routes and runways may parallel the stream or cross it. Streams are used for escape, daily movements, and dispersal (Anderson et al. 1976, Ludwig 1981). Many smaller alpine streams used by water voles are ephemeral and depend upon melting snow and precipitation for their existence. Water voles are rarely captured away from water (Pattie 1967, Ludwig 1981, Klaus et al. 1999, Klaus 2003), but they are probably able to disperse short distances overland

(Klaus et al. 2001). Sex and age specific differences in dispersal are not known.

Annual activity patterns and movements

Although there is little hard data on the subject, it is assumed that adult water voles maintain home ranges for as long as possible and move only in response to major changes in habitat or displacement by more aggressive individuals. Seasonal shifts in home ranges are not known to occur (Ludwig 1981). Adults occupy rather linear home ranges that stretch out along streams (Pattie 1967, Anderson et al. 1976, Ludwig 1981, Klaus et al. 1999). In the Shoshone National Forest, adult females stayed within exclusive linear home ranges of up to 67.1 m; adult males used stream lengths up to 463 m (Klaus et al. 1999). In Alberta, Ludwig (1984a) reported mean home ranges of 222 ± 76 m^2 for over-wintered adult females and 770 ± 359 m^2 for over-wintered adult males. The mean adjusted range length for both sexes of water voles in the Beartooth Mountains was 118.87 m (Pattie 1967). The home ranges of males overlapped the seasonal ranges of both adult females and adult males, but adult female home ranges were exclusive of other adult females (Anderson et al. 1976, Ludwig 1984a, Klaus 1997).

In both the Shoshone and Bighorn National Forests, juvenile water voles from the season's first litter (born mid-June) presumably leave their natal sites by mid- to late-July (Pattie 1967, Klaus et al. 1999, Klaus 2003). In the Shoshone National Forest, juvenile water voles have been captured not only in their expected habitat, but also along lakes and beside large, steep, fast flowing streams (Klaus 1997). Initially, dispersal or migration was thought to be limited primarily to stream networks (Ludwig 1981), but overland migration between adjacent watersheds is likely (Klaus et al. 2001). Low genetic distances were calculated between water voles captured from four adjacent headwater basins in the Shoshone National Forest (Klaus 2003). The direct overland distance between sampling locations was short in comparison to water routes, which included large waterfalls, swift currents, and many kilometers of low elevation stream lacking the habitat characteristics preferred by water voles. This evidence, coupled with their relatively short 16-month lifespan and the severity of winters throughout the region, suggests that water voles can move relatively short overland distances between adjacent watersheds (Klaus et al. 2001). Such inter-watershed dispersal may be greatest during very wet periods, when ephemeral drainages and side channels become more suitable for water voles.

Water voles probably can re-colonize vacant patches of suitable habitat from nearby occupied patches, although specific distances, patch sizes, and dispersal frequencies are unknown. In the Bighorn National Forest, water voles were regularly captured within the Fool Creek exclosure; but when the exclosure was removed, no water voles were captured. When the exclosure was replaced, water voles were again captured at the site (Blankenship 1995, Klaus 2003). The re-colonization distance was probably short, but the source population is unknown.

The Shoshone National Forest supports a relatively large amount of actual and potential habitat, and also apparently supports a large number of water voles, which suggests a relatively high probability that the species will persist here for some time. Long term viability of water voles on the Shoshone National Forest is further increased by the potential immigration of individuals from populations to the north in Montana, to the west in Yellowstone National Park, and to the south in the Bridger-Teton National Forest. Water voles from Quad Creek, Montana in the Custer National Forest (USDA Forest Service Region 1) and from the Shoshone National Forest were genetically indistinguishable, suggesting population connectivity across the state border (Klaus et al. 2001). The Shoshone and Custer National Forest water voles in the Rock Creek watershed had a fixation index of zero (F_{ST} = 0), indicating no loss of heterozygosity and little genetic differentiation (Wright 1978, Klaus et al. 2001). When F_{ST} equals zero, the number of migrants/subpopulation/generation (N_m) is sufficiently high to prevent genetic differentiation (Hartl and Clark 1989). There are no data regarding relatedness of water voles on the border of the Shoshone National Forest and Yellowstone National Park, or the Shoshone and Bridger-Teton National Forests. It is assumed that water voles in these areas are related to degrees similar to that documented on the Montana border.

However, genetic distances between water voles in the Beartooth Mountains and those 150 miles away at Togwotee Pass in the Absaroka Mountains were significantly different, suggesting that water vole genes do not readily disperse across this distance, even though these areas are connected by contiguous boreal habitat (Klaus et al. 2001). Based on these limited data it appears that successful overland migration is infrequent enough that large overland divides, and perhaps the cumulative distance of a series of smaller divides, are sufficient to parse water voles into genetically distinct units.

Also, it is likely that large, low-elevation basins are complete barriers to water voles. Brown (1971) found that dry, low elevation environments were barriers to most small boreal mammals, and that "… a few thousand feet of elevation, with the associated differences in climate and habitat, constitute a nearly absolute barrier to dispersal by small mammals (with the exception of bats)." He noted that there have been post-Pleistocene extinctions, but no colonizations, of boreo-alpine mammals in the Great Basin. The continental distribution of water voles (**Figure 4**) clearly shows their absence from the dry and low habitats of the interior Columbia River Basin. By extension, immigration of water voles (and other small boreal mammals, such as southern red-back voles and red squirrels) to or from isolated mountain ranges like the Big Horn Mountains is unlikely. Potential routes of dispersal to the Big Horns cross approximately 140 km of cold desert (Big Horn Basin), 130 km of dry, low, and treeless mountains with very few permanent streams (Owl Creek and Bridger Mountains), or 75 km of short grass prairie (Pryor Mountains vicinity) (**Figure 1**). The water vole population on the Big Horn Mountains is best described as a Pleistocene relict that has been isolated to that range for several millennia. As discussed previously, this raises the possibility of significant genetic differentiation of the Big Horn mountain population, possibly to the point of subspeciation (Beauvais 2000).

Habitat selection and use

Habitat quality can be inferred from the behavioral choices of individuals as they recognize and select sites to occupy. For many vertebrates, patterns of abundance, intensity of use, and habitat preference are reliable indicators of the environments needed for population persistence (Ruggiero et al. 1988). In some cases, population density can be decoupled from habitat quality. However, according to the criteria of Van Horne (1983), water vole density should positively correlate with habitat quality. Specifically, water voles are habitat specialists that do not seasonally change their home ranges.

Water voles have rather narrow habitat requirements. Preferred sites occur in a disjunct pattern of short, fragmented patches along reaches of alpine and subalpine streams (Pattie 1967, Ludwig 1981, Reichel 1986, Klaus 2003). In general, they are found in linear colonies along spring-fed or glacial streams with gravel bottoms and about 5° slope (Ludwig 1981, Klaus 2003). The stream channels are usually narrow and bordered

by deep soil layers used for burrowing (Ludwig 1984a; **Figure 9**).

Of ten habitat variables analyzed by Ludwig (1981), three were important for separating occupied from unoccupied sites: percent stream gradient, the number of openings in the stream bank not produced by rodents, and soil depth. Occupied sites had stream gradients that averaged 6.54 ± 1.14%, number of openings averaging 5.30 ± 0.92, and soil depths averaging 38.01 ± 6.62 cm. Unoccupied sites were steeper (8.84 ± 0.90%), had fewer openings (4.58 ± 0.46), and shallower soils (30.34 ± 3.08 cm). Stream characteristics did not vary significantly between occupied and unoccupied sites. Occupied sites had stream widths averaging 154.5 ± 26.9 cm, stream depths averaging 7.91 ± 1.4 cm, and stream velocities averaging 0.39 ± 0.07 cm/sec. Unoccupied sites were

similar in all of these aspects (width 152.8 ± 15.51 cm; depth 7.91 ± 0.8 cm; velocity 0.39 ± 0.40 cm/sec).

Water vole burrows have large entrances with lateral surface openings 12.7 to 15.2 cm in diameter (Hollister 1912). Burrow entrances are in the stream bank, at water level (**Figure 6**), or occasionally submerged. Minor temperature variations were found within burrows (Pattie 1967). Water vole tunnels 6 cm wide can be found below plant roots and mosses (Ludwig 1999).

About 75 percent cover by mid-to-late seral vegetation, dominated by willow, sedges, grasses and forbs immediately adjacent to the stream, appears to be important for water voles (Pattie 1967, Anderson et al. 1976, Brown 1977, Ludwig 1981, Getz 1985, Reichel 1986, Anthony et al. 1987, Blankenship 1995,

Figure 9. Occupied water vole (*Microtus richardsoni*) habitat along a tributary to Long Lake, 3063 m elevation, Shoshone National Forest, Wyoming. More water voles were captured at this location in 1990 and 1991 than at any other trapped site in the Beartooth Mountains. Photograph by M. Klaus.

Klaus 2003). Water voles prefer locations inhabited by previous generations of water voles (Ludwig 1981). Examples of water vole habitat in the Shoshone National Forest are provided in **Figure 8** and **Figure 9**. An example of habitat in the Bighorn National Forest is provided in **Figure 10**.

Water voles generally remain within 17 m of open water (range 11.6 - 16.7 m), even though a few animals may move further away into adjacent wet areas (Ludwig 1984a). It is clear that this association with permanently wet habitat is real and not an artifact of spatially-biased sampling. There is a rather long tradition of small mammal trapping in the uplands of national forests in the Rocky Mountains, including those in Region 2 (e.g., Beauvais 1997), and water voles have not been documented anywhere but in permanently wet sites. Water vole inventories have focused mostly on streamside meadows. Other wet habitats such as peatlands and marshes have received less survey effort, and water vole use of these habitats is less well known.

In Washington, Reichel (1986) captured water voles only in wet meadow and willow habitats with greater than 75 percent vegetation cover. In old growth and mature forests in the western Cascade Range of Oregon, Doyle (1987) captured water voles on stream segments where cover by Douglas-fir (*Pseudotsuga menziesii*) was sparse and where a number of recently fallen logs were present. Captures on stream segments in old growth stands were significantly more frequent than on those in mature forest stands, but the most positively correlated variable was the percent of exposed soil (Doyle 1987). However, in the Bighorn National Forest, bare ground had low correlation ($r^2 = 0.25$) with water vole captures, no captures occurred on stream segments under tree canopies, and fallen logs were rarely encountered next to streams (Klaus 2003).

Figure 10. Occupied water vole (*Microtus richardsoni*) habitat at Bald Mountain Creek, 2743 m elevation, Bighorn National Forest, Wyoming. This is a Rosgen Class B stream with a willow/wet *Carex* riparian classification. In August, when this site is grazed, cattle were observed to trail around the streamside willows which helped to preserve the soil structure in the stream bank. A total of 22 water voles were captured here, more than at any other location in the Big Horn Mountains. This was the only site where water voles were captured early in the season (June), when this photograph was taken. Photograph by M. Klaus.

In the Shoshone National Forest, water voles were trapped exclusively along streams (Pattie 1967, Klaus et al. 1999). They occupied hummocks bordering streams and were most frequently captured near hummocks covered by dense stands of willow or along streams with undercut banks (Pattie 1967, Klaus 2003; **Figure 8** and **Figure 9**). In the Bighorn National Forest, the best locations for capturing water voles were on streams above 2,440 m with Rosgen B or E classifications. Type B channels are riffle dominated and moderately entrenched with moderate width-depth ratio and sinuosity; type E have gentle gradient, riffle/ pool type channels that are slightly entrenched with a very low width-depth ratio and a very high sinuosity (Rosgen 1994, 1996). Both of these channel types have a water surface slope ranging from 2 to 4 percent. Most water voles were captured in the willow/wet *Carex* riparian type (Girard et al. 1997, Klaus 2003; **Table 2**). The willow/wet *Carex* type is found on relatively undisturbed sites with stable well-developed soils and bank structures (Girard et al. 1997).

Percent cover by willows did not correlate significantly with water vole abundance in the Bighorn National Forest, but they did provide protective cover (**Table 3**, **Figure 10**). Willows were an important habitat component for water voles at the Rooster Hill Exclosure (Bighorn National Forest) where the stream depth was unusually shallow (Klaus 2003; **Table 2**) and at Bald Mountain Creek (Bighorn National Forest) where cattle were observed to trail around willow covered hummocks (**Table 3**, **Figure 10**). When willows are well established along the stream to provide escape cover, water depth did not appear critical to

water vole survival or reproduction (**Table 2** and **Table 3**). At the Rooster Hill Exclosure (Bighorn National Forest), the mean water depth was only 1.85 cm, less than previously reported for streams occupied by water voles (Ludwig 1981). At this site, released water voles invariably ran into the dense willows that line each side of the stream, because the stream itself was too shallow to be used for escape. At Bald Mountain Creek (Bighorn National Forest), water voles were primarily captured within the willows where bank structure was intact. Bald Mountain Creek (Bighorn National Forest) is a good example of the willow/wet *Carex* riparian type in the Bighorn National Forest (**Figure 10**). While water voles were captured on streams in the Bighorn National Forest that do not have willows, such as Fool Creek, it is not known whether willow cover could be used to predict the probability of their occurrence at a site (**Figure 11**). Anderson et al. (1976) successfully captured water voles in sites abundant in moss and willow, some reaching 250 cm in height. In winter, willows may improve the subnivean environment for water voles by trapping and suspending snow, thus preventing it from packing too hard. This would provide both thermal protection and a substratum for burrowing (Birney et al. 1976).

Percent cover by ferns and thallophytes (mosses and liverworts) correlated positively and significantly (ferns $r^2 = 0.87$, P = 0.007; thallophytes $r^2 = 0.80$; P = 0.017) with the abundance of water voles in the Bighorn National Forest, despite the fact that these plants are not known food sources for water voles and grow too low to the ground at high elevations to function as cover (Klaus 2003; **Table 3**). Because these plants require external

Table 2. Habitat characteristics and ecological densities of water voles (*Microtus richardsoni*) at sites in the Bighorn National Forest, Wyoming. From Klaus (2003).

Site	Elevation (m)	Aspect	Rosgen stream class[a]	Riparian class[b]	Mean water depth (cm)[c]	Ecological density of water voles[d]
Bald Mountain Creek	2743	40° NE	B	Willow/wet *Carex*	35	24
Duncum Creek	2572	48° NE	G	Dece/Forb and Cami/Dece	27.9	3
Fool Creek	2484	78° NE	B	Cami/Dece	21.5	9
Fool Creek Exclosure	2490	90° E	B	Cami/Dece	17.0	15
Rooster Hill Exclosure	2798	72° NE	E	Willow/wet *Carex*	1.85	57
Wyoming Gulch Creek	2804	22° NE	E	Popr/Taof and Dece/forb	21.1	12

[a]Mandrella (2001)

[b]Beard (2001) and Bischoff (2001); Dece = *Deschampsia cespitosa*, Cami = *Carex microptera*, Popr = *Poa pratense*, Taof = *Taraxacum officinale*

[c]Mean of means; N = 6

[d]No. water voles/ mean distance trapped x 1000

Table 3. Mean percent cover (±SE) and dry weight of vegetation (g) at sites occupied by water voles (*Microtus richardsoni*) on the Bighorn National Forest, Wyoming. The coefficient of determination (r^2) refers to the linear regression of the relative abundance of water voles on the habitat values in each row. From Klaus (2003).

Plant life form[a]	Bald Mountain Creek (grazed)	Duncum Creek (grazed)	Fool Creek (grazed)	Fool Creek Exclosure (ungrazed)	Rooster Hill Exclosure (ungrazed)	Wyoming Gulch (grazed)	(r^2)[d]
Thallophytes[b]	16.7±0.2	12.0±4.1	19.9±12.4	15.8±15.6	34.7±27	2.0±0.7	0.80
Horsetails	0.1±0.1	5.3±3.3	0.0	0.13±0.125	0.3±0.2	4.6±3.5	0.30
Ferns	0.0	0.0	0.0	0.0	0.02±0.2	0.0	0.87
Graminoids	17.9±10.5	5.25±2.6	22.5±9.5	34.6±13.3	6.5±6.2	1.7±0.8	0.01
Forbs	7.7±4.8	9.4±4.3	16.0±7.5	37.1±19.2	24.7±10.3	11.3±6.5	0.20
Shrubs	54.2±17.6	4.6±3.5	0.0	0.0	63.3±24.2	22.6±21.6	0.50
Litter	33.0±13.8	20.6±5.6	21.0±12.2	47.0±18.6	31.2±28.2	16.7±16.2	0.20
Bare ground or rock	2.5±2.5	3.8±3.8	2.3±2.12	0.13±0.1	0.0	0.4±0.4	0.25
Mean[c] dry weight biomass	148.6	58.5	40.7	47.4	194.7	66.9	0.25

[a]Whittaker (1975)

[b]Mosses and liverworts

[c]Mean of means; N = 6

[d]The coefficient of determination (r^2) refers to the linear regression of the relative abundance of water voles on the habitat values in each row.

water for reproduction, they may simply indicate a high water table and available surface water; in other words, the correlation is likely a secondary indication of the water vole preference for wet sites. Percent cover and height of grasses and forbs were not significant (**Table 3**). This suggests that stubble height, which is used to monitor grazing pressure in the Bighorn National Forest, is probably not strongly related to water vole habitat needs.

Seasonal habitat use

During all seasons water voles use sites that are well drained and have a deep soil layer next to a stream (Ludwig 1981). At high elevations, water vole habitat patches are under snow up to eight months annually, with snowfall possible anytime. A short summer growing season of three to four months is typical at these high elevations. When snow cover accumulated to about 6 cm, water vole activity became primarily subnivean. They excavate tunnels through the snow and subnivean nests are found on the soil surface. These nests may be used either during the winter or only during the spring thaw when underground areas flood (Dalquest 1948, Ludwig 1981, 1984a).

Nests

Water voles use nests year-round. These may be located in hummocks, underneath logs, or below stumps (Ludwig 1981, 1984a). Nests found within underground burrows were constructed of 2 to 5 cm pieces of various grasses (*Agropyron*, *Calamagrostis*), sedges, and rushes (*Juncus*) (Ludwig 1981). A single water vole uses one spherical nest, with an interior cavity of about 7 cm in diameter (Ludwig 1984a). It is assumed that flooding periodically causes some nests to become at least temporarily unusable.

In captivity, water voles built nests that were uniform, spherical and hollow in the center (Erickson-Pallett 1992). Dry nests built by males and females did not vary in thermal conductance (0.55 cal/cm^2 hr ^{0}C) and were estimated to provide a 29.7 percent energy savings to the animal (Erickson-Pallett 1992). These values were not scaled temporally for winter and apparently represent general year-round estimates.

Food habits

Water voles are primarily herbivores that feed on both aboveground and belowground plant material (Ludwig 1984a, Batzli 1985), and their teeth are adapted to a bulky diet of abrasive grasses and forbs (Anderson 1959). Leaves and sometimes stems of different forbs comprise the major part of their summer diet (Ludwig 1981, 1984a). They also eat grasses, sedges, willows (buds and the inner bark of twigs), seeds (*Vaccinium* and conifer), bulbs (*Erythronium*), and small amounts of insect matter. Diet varies throughout water vole range
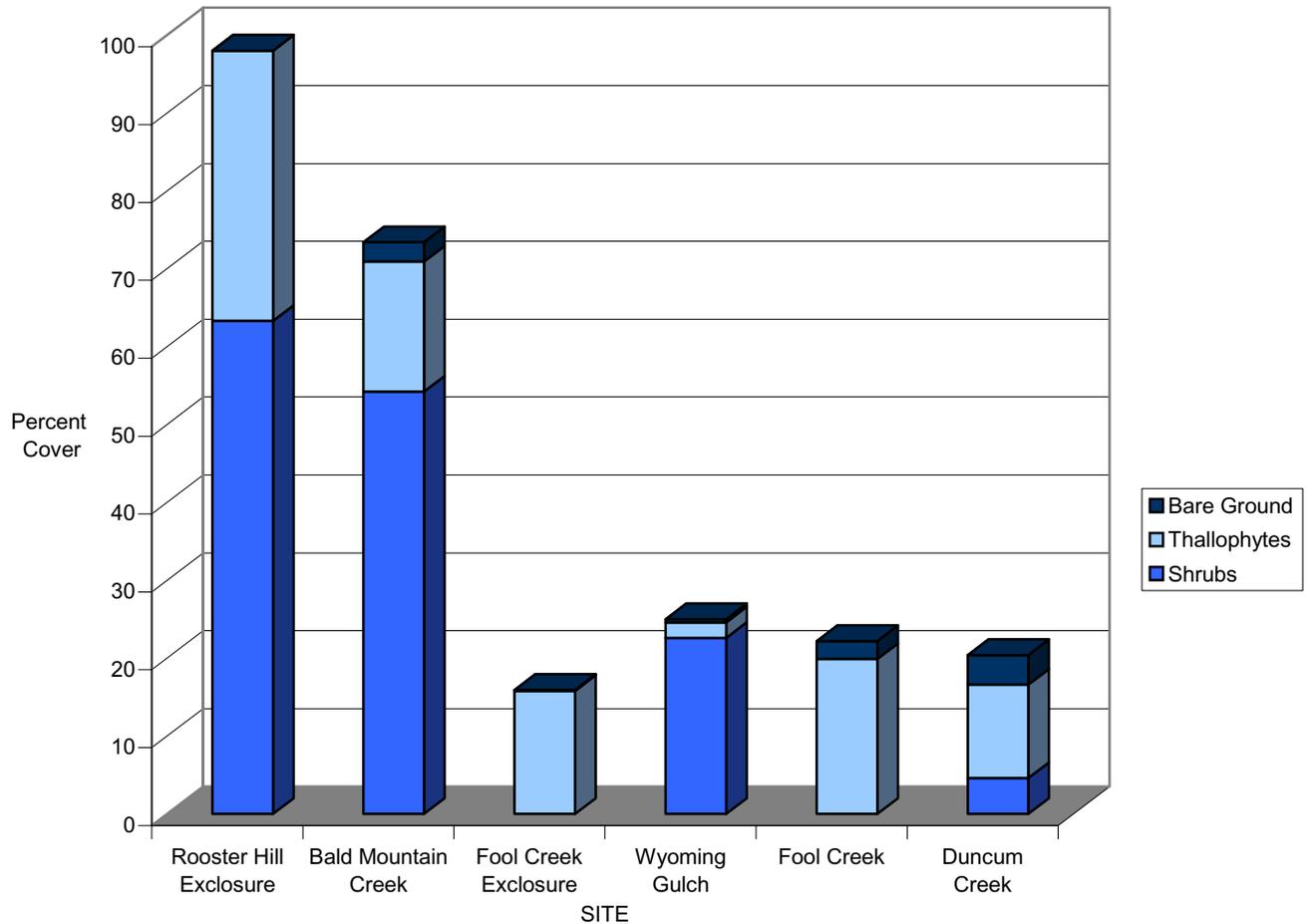
Figure 11. Percent cover of shrubs, thallophytes, and bare ground at sites occupied by water voles (*Microtus richardsoni*) in the Bighorn National Forest, Wyoming. Rooster Hill Exclosure and Bald Mountain Creek had the highest percent cover of shrubs (willows), and also had the highest capture success for water voles in the northern Big Horn Mountains. More information on vegetation at these sites is presented in **Table 3**.

(Anderson et al. 1976, Ludwig 1984a, 1999, Clark and Stromberg 1987, Foresman 2001). In Alberta water voles ate the dried aerial parts of various herbaceous plants, buds of perennials, rhizomes, corms, and roots of willow, *Pedicularis*, *Arnica*, *Antennaria*, *Xerophyllum tenax* and *Erythronium gradiflorum* (Ludwig 1981, 1984a, 1999). Surface digging for belowground material has not been observed, and moss was not found in their food piles (Ludwig 1981). In captivity water voles were successfully fed rabbit chow, rat-mouse-hamster chow, cracked corn and other grains, sunflower seeds, apples, lettuce, and carrots (Jannett and Jannett 1974, Jannett et al. 1979, Erickson-Pallett 1992). Apparently water voles do not store food for the winter.

Water voles probably shift food preference in response to seasonal changes in the nutritional value of different plant species (Ludwig 1981, Batzli 1985).

As plants age, their aerial portions lose fat, protein, and phosphorus, while levels of fiber and calcium increase. In one study of water vole diet, Ludwig (1981) found no significant difference between the nutrient levels of food and non-food plants. Water voles tend to have higher metabolic rates, consume fewer calories per gram of body weight, and digest their food more efficiently than predicted (Ludwig 1984a).

Carleton (1981) summarized the major characteristics of the water vole digestive system. The stomach is similar to other *Microtus* and unlike *Arvicola*. While prismatic teeth, ever-growing molars, and large caeca adapt water voles for digesting fibrous plant material, they generally digest seeds more efficiently than the vegetative parts of plants. Seasonally, seeds and insects may form a significant part of their diet.

The relative abundance of certain dietary items probably results from their availability within the local environment. Food quality may partially explain variations in population density between locations, seasons, and years (Batzli 1985). No information is available on age specific food preferences or differences, and no study of diet has been conducted in Region 2.

Breeding biology

Water voles preferentially occupy areas occupied by previous generations of water voles, while similar nearby sites remain unoccupied. Water voles appear to have a high degree of site fidelity throughout the year, presumably because specific habitat features are crucial for survival and reproductive success (Ludwig 1981). Females capable of occupying high-quality sites produce litters, while female "floaters" in peripheral, lower quality sites apparently do not (Ludwig 1988). In general, female water voles occupy non-overlapping home ranges, while males use home ranges that overlap several females. Water voles probably mark their home ranges with scents from their feces, urine and flank glands and likely defend these areas actively. Wounds from aggressive encounters were found on 76 percent of adult male water voles and up to 20 percent of adult female water voles; although failed predation events could not be ruled out as the causes of these wounds, at least some were likely from intraspecific interactions (Ludwig 1984a).

Temperature, light, nutrition, and social factors are known to influence reproduction in rodents (Batzli et al. 1977). Temperature differences were not significant between the sites used for reproduction and those that were not used (Ludwig 1984b). Spring floods caused by melting snow did reduce the total number of sites used by females for nesting and reproduction (Ludwig 1984a).

Male water voles have a baculum (Os penis) with a broad stalk 3.7 to 4.3 mm in length and four times longer than the median process with one median ossified process (Anderson 1960, Ludwig 1984a). The baculum is unique and may be used for species identification (Anderson 1960). Throughout the summer, adult males had enlarged testes with numerous sperm (Brown 1977). Males display a distinctive drum marking behavior, a characteristic shared with *Arvicola* species. They rub their flank glands with a hind foot and then repeatedly stamp the ground. No such behavior has been observed in other species of *Microtus*. Drum marking, flank rubbing, anal drag, and pelvic press are androgen-dependent behaviors observed in captive male water voles (Jannett and Jannett 1974, Jannett et al. 1979).

Over wintered adult females in preferred habitat patches produce litters in June, July, and August (Pattie 1967, Anderson et al. 1976, Ludwig 1984a, Klaus et al. 1999). Ovulation is induced in females during late May and early June when vegetation begins to green (Brown 1977, Ludwig 1984a). There is no evidence for spontaneous ovulation (Jannett et al. 1979). In captivity, the minimum gestation period was 22 days (Jannett et al. 1979). The first litters are born in late June or early July (Pattie 1967, Brown 1977, Ludwig 1984a, Klaus et al. 1999). Adult females typically produce two (Brown 1977, Ludwig 1988) or three (Pattie 1967, M. Klaus unpublished data) litters during the breeding season, generally ranging from four to seven pups per litter (Hall and Cockrum 1953). In the Shoshone National Forest, juvenile water voles weighing 13 to 49 g were captured in July, August, and as late as the second week of September, suggesting that three litters were produced during the breeding season (Pattie 1967, M. Klaus unpublished data,). Copulation occurs as early as the first day after parturition (Jannett et al. 1979). In both the Shoshone and Bighorn National Forests capture rates were low until the middle of July when adults as well as young from the first litter were trapped. Water voles are probably the most vulnerable to disturbance during their reproductive season, but this has not been studied. In early spring and summer, the burrow soil is moist and may be compacted more easily when trampled than later in the summer when the soil is drier (Klaus et al. 1999, Klaus 2003).

Water voles weigh about 5 g at birth, and although they are born both naked and blind, they can vocalize. By day 3, they are sparsely covered with fur and their pinnae stick out from their head. By day 6 they have incisors. Even though they are able to run and climb by day 10, their eyes do not open until day 12 when they are able to run fast. Captive water vole pups swam voluntarily by day 17 and were weaned by day 21. The testes descended by day 38, and captive pups nested separately by day 40 (Ludwig 1984a). There is almost nothing known about parental care in water voles.

Dispersal of young

As discussed previously, juvenile water voles are known to nest independently 40 days following birth; those from the season's first litter (born mid-June) are thought to disperse at about this same age in mid- to late-July. Most dispersing individuals probably move along waterways, but overland travel is possible, especially

during wet periods (Pattie 1967, Ludwig 1981, Klaus et al. 1999, Klaus 2003). Dispersal distances are essentially unknown, as are differences in dispersal dynamics between individuals born at different times during the summer.

Demography

The small amount of existing information on water vole demography has been gathered via trapping studies and by analyzing the genetics of trapped individuals. Standard tools (e.g., Museum Special snap-traps, Sherman live traps) and techniques (e.g., linear trap lines, two-dimensional trap grids) of small mammal investigation have been employed in these efforts, but it is important to recognize that information gathered by trapping is not necessarily representative of a given population.

The number of pups per litter varies by study: 7.85 ± 0.51 (± SE) (Brown 1977), 4 to 7 (Hall and Cockrum 1953), 5.52 to 6.11 (Ludwig 1981), 6.00 (Negus and Findley 1959), and 7.00 (Racey and Cowan 1935). In the Shoshone National Forest, young per litter (± SE) was 5.45 (Pattie 1967) and 5.75 ± 0.54 (drier summer) to 7.75 ± 0.63 (wetter summer) and 6.4 ± 0.61 (ungrazed site) to 7.0 ± 0.58 (grazed site) (Klaus et al. 1999). Adults and older juveniles produce larger litters (Pattie 1967, Ludwig 1981), and thus some of the variation reported above may be due to varying age classes of the females involved. The mean number of embryos reported by Pattie (1967) is close to the mean reported for drier summers by Klaus et al. (1999), suggesting that female fecundity has remained stable in this area of the Shoshone National Forest for the past 30 years. During an exceptionally wet breeding season, there were significantly more embryos in trap-killed females (t = 2.67, df = 5, P < 0.05), significantly greater mean weights of the youngest males (U = 191.5, P < 0.002), and significantly increased capture success (U = 110.5, P < 0.04) in the Shoshone National Forest (Klaus et al. 1999).

Spatial character of populations in USFS Region 2

Water vole populations in the Rocky Mountains are clearly discontinuous at several scales, suggesting that a metapopulation perspective might help in understanding the taxon in Region 2. To understand and predict population dynamics based on metapopulation theory, four basic conditions should apply: (1) suitable habitat should occur in patches, (2) even the largest populations in an area should have an ample risk of extinction, (3) re-colonization must be possible, and (4) local populations should vary in their dynamics (Hanski and Gilpin 1997). Inherent in this concept is the view of space not only as a discrete geographic area, but also as containing distinct suitable and unsuitable habitat patches where colonization, extinction, and re-colonization events occur. Metapopulation theory may be applicable to water voles, but there is simply too little information on the species to confidently state that water voles form formal metapopulations. Clearly, water vole populations are subdivided into small colonial groups living in discrete habitat patches along high elevation streams, and successful colonization and re-colonization events are possible because stream corridors link preferred habitat sites within a watershed and water voles can likely move short distances overland between adjacent watersheds. However, until more information is gathered on the extent to which (1) dispersal connects patches of suitable habitat, and (2) population dynamics in separate patches are asynchronous, water vole populations are probably best referred to as "patchy populations" rather than metapopulations.

In the Shoshone National Forest, the extent of water vole isolation between habitat patches within and between watersheds was estimated using allozymes and mtDNA restriction data. The average proportion of polymorphic allozyme loci for *Microtus richardsoni macropus* in the Shoshone National Forest was estimated to be 0.06 (Klaus et al. 2001), low in comparison to the average proportion of 0.45 for *M. r. richardsoni* (Anderson et al. 1976) and 0.43 for *M. r. arvicoloides* (Petcoff 1985). The mean fixation index (Wright 1978) for water voles from four adjacent headwater basins, two on either side of Beartooth Pass in the Shoshone National Forest, was 0.11, indicating a moderate amount of genetic differentiation. The mean number of migrants/subpopulation/generation was large enough to suggest gene flow across the four adjacent headwater basins (Klaus et al. 2001).

Restriction analysis of mtDNA isolated from water voles in the Beartooth Mountains yielded 29 different haplotypes from 142 individuals (Klaus et al. 2001). The number of unique haplotypes and their frequencies were similar to those reported for *Microtus pennsylvanicus* (Plante et al. 1989). Debry (1989) found two different haplotypes that differed at three sites for four individual water voles from Red Cliff campground near Big Sky, Gallatin County, Montana. Most mtDNA haplotypes isolated from water voles captured in the Shoshone National Forest were localized geographically by watershed, whereas all shared haplotypes, except for one, came from animals captured at geographically

contiguous locations (Klaus et al. 2001). There was no evidence for geographic isolation or genetic structuring among water voles captured in four adjacent headwater basins of the Shoshone National Forest (Klaus et al. 2001). The overland distances between headwater streams in these watersheds was <15 km, whereas the hydrological connection between streams in these watersheds ranged up to 296 km. This indirectly implies that water voles are capable of migrating to habitats along streams of one watershed as well as between adjacent watersheds, and inter-watershed recolonization following a local extinction is possible.

Genetic distances estimated from water voles captured on the east and west sides of Togwotee Pass (overland distance approximately 10 km) were not significantly different even though the pass is on the continental divide and no stream confluence exists as a migratory corridor between the two sides. The average genetic distance between water voles from both the east and west sides of Togwotee Pass and those from all four watersheds sampled in the Shoshone National Forest was significant and estimated to be 0.02 (Klaus et al. 2001). These data suggest that although water voles can move short distances overland, movements across longer distances and between major mountain ranges, even when such ranges are connected by contiguous boreal habitat, is very limited. Movement across low elevation areas of unsuitable habitat is assumed to be even more unlikely.

Demographic imbalances, loss of genetic variation, environmental stochasticity, and deterministic threats, such as loss of habitat, may cause local extinctions, especially of small populations (Hanski and Gilpin 1997). Because the Big Horn Mountains are an island mountain chain surrounded by low elevation basin environments, and because water voles are distributed in a rather discontinuous manner throughout only a small portion of the stream network on the mountain range, water voles in the Bighorn National Forest are probably best described as a series of small and geographically isolated populations, each of which is susceptible to demographic, genetic, and environmental processes that can cause extinction (Brown 1971, Soule 1987, Hanski and Gilpin 1997). The boreal habitat on the Big Horn Mountains has been isolated from other regions of boreal habitat for the past 8,000 to 10,000 years. Water vole populations in the Big Horns probably have not received genetic input from other populations for several thousand generations, and they may represent a distinct evolutionary unit, possibly subspecies. This has not been studied, and further investigation is needed

to understand the intra-species differentiation of water voles in Region 2.

Life history characteristics

Water voles are slow to mature relative to other small mammals. Juveniles commonly do not breed in their first summer, but instead they mature over the winter to become breeding adults the following spring (Ludwig 1981). Ludwig (1988) estimated 25 percent of juveniles were reproductive in the season which they were born, and juvenile water voles matured sexually at an earlier age depending upon levels of precipitation (Klaus et al. 1999). During one exceptionally wet summer in the Shoshone National Forest, 51 percent of the youngest males and 32 percent of the youngest females weighing 13 to 49 g showed signs of reproductive activity, while all of the mid-weight juveniles, 50 to 69 g, were reproductive. During drier summers, none of the youngest group and only a few mid-weight juveniles showed signs of reproductive activity (Klaus et al. 1999). By August, juvenile males were sexually mature and most juvenile females bred the year they were born (Pattie 1967). Negus and Findley (1959) described one pregnant female that weighed only 34 g and found sperm in males weighing 28 g. Jannett et al. (1979) found mature follicles and perforate vaginas in water voles weighing 35.7 ± 5.3 (SE) g. Among the 13 to 49 g juveniles captured in the Bighorn National Forest, 57 percent in grazed and 42 percent in ungrazed areas had signs of reproductive activity. Among the mid-weight juveniles, 60 percent in grazed and 62 percent in ungrazed areas showed signs of reproductive activity (Klaus 2003). Adults and older juveniles have more offspring per litter; sex ratios of litters apparently do not differ by age class (Pattie 1967, Ludwig 1981).

Although water vole densities usually remain low, water voles have high reproductive potential resulting from induced ovulation, postpartum estrus, and lactational pregnancies (Ludwig 1988). Water voles can respond to improved environmental conditions (e.g., increased precipitation) with a rapid increase in reproduction and abundance (Racey 1960, Klaus et al. 1999). More embryos per trap-killed female were found and capture success increased significantly when precipitation levels were high (Klaus et al. 1999). Effects of this irruption in subsequent years are not known.

In the alpine environment, where the breeding season is short and the weather is often harsh, water

voles typically produce a limited number of offspring (Ludwig 1988). Ludwig (1981) suggested that natural selection in such an environment has caused water voles to produce fewer but higher-quality offspring, as opposed to the more iteroparous strategy typical of most small mammals. At best, water voles overwinter only once and die during their second fall or winter (Ludwig 1984a). Overwintered adult females usually die either during the summer or fall, and few reproduce throughout the entire breeding season (Ludwig 1988). One radio-collared female lived an estimated 16 months (Ludwig 1981). In comparison to *Microtus* species inhabiting more moderate climates, overwintered female water voles produce fewer and more moderately sized litters per year, and relatively few juveniles reproduce the summer of their birth (Ludwig 1988). Nevertheless, populations of water voles occasionally do irrupt (Racey 1960, Klaus et al. 1999). More information is needed in this area of their biology.

Gross mortality (death and emigration) among water voles in Alberta ranged between 71.4 and 100 percent, with juveniles replacing adults at a rate of 1:1 or greater (Ludwig 1984a). Over a three year period, Ludwig (1981) reported 88.9 percent mortality of overwintered adults by the end of September. This is presumed to be an annual rate from September to September. Pattie (1967) found evidence for prenatal mortality. Because of high mortality, water vole populations typically remain low.

Life cycle model

Description and general results

Matrix population analyses are often used to help identify particular cohorts and vital rates that have disproportionately large effects on population growth. We have employed such a matrix analysis to better illustrate water vole populations. However, we caution that the accuracy of any population model depends almost entirely on the accuracy of the data used to parameterize the model. The paucity of field data on water voles forced us to use a combination of data from small-scale studies of water voles and, in a few cases, data on vital rates of similar species to parameterize this model. Thus, we view our model results as a best approximation under the constraints of existing information and strongly suggest that although the model results have broad management utility, more research into water vole population structure and vital rates is definitely needed to more completely understand their population dynamics.

A life cycle graph (**Figure 12**) for the water vole provides the basis for a matrix population analysis (Cochran and Ellner 1992, McDonald and Caswell 1993, Caswell 2000) conducted by McDonald and Ise (2002). The model has three kinds of input terms: P_i describing survival rates, B_i describing probabilities of additional breeding events (breeding as young of the year or having second and possibly third litters as a yearling), and m_i describing fertilities (**Table 4**). The values assigned to P_j, B_j, and m_i may represent maximal or near maximal growth for water voles. An alternative model with different P_j, B_j, and m_i values might give a somewhat different picture of population sensitivities and elasticities. **Table 5** shows the projection matrix corresponding to the life cycle graph. The population growth rate, λ, was 1.238 based on the estimated vital rates used for the matrix. Although this suggests a growing population, the value is subject to the many assumptions used to derive the transitions and should be interpreted with caution.

Sensitivity and elasticity analyses

A more useful indication of the state of the population comes from the sensitivity and elasticity analyses. One of the most important aspects of these analyses is their ability to identify portions of the life cycle that have large potential influences on growth and thus should be the focus of data collection. Highly sensitive or elastic transitions have a large impact on λ – errors of estimation for the corresponding vital rates will have the greatest effect on the conclusions of the model. The effect on λ of an absolute change in the vital rates (a_{ij}, the arcs in the graph and the cells in the matrix) predicts that λ of water voles is most sensitive to changes in early reproduction by early newborns (Node 1 back to Node 1: 0.727) followed by mid-season reproduction of early newborns (from Node 1 to Node 2: 0.485) and early reproduction of middle newborns (Node 2 to Node 1; 0.388). **Table 6** has the possible sensitivities only matrix for this analysis (one can calculate sensitivities for non-existent transitions, but these are usually either meaningless or impossible).

It is important to note that the above three sensitive cases refer to reproduction by water voles in the season <u>following</u> their birth, and not in the season <u>of</u> their birth. This same qualification holds for the below discussion of elasticity.

Elasticity (**Table 7**) is the effect on λ of proportional changes in the vital rates (the arcs in the graph and the cells in the matrix). The elasticities
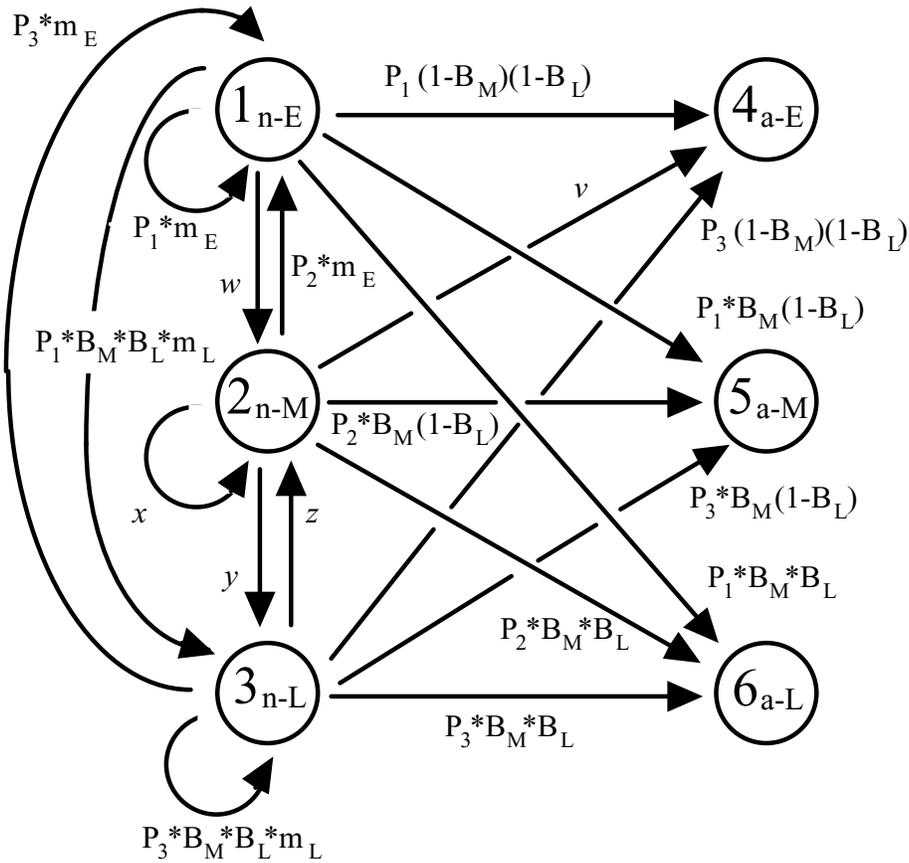
Figure 12. Life cycle graph for the water vole (*Microtus richardsoni*), with three stages for newborns (Stages 1 - 3 followed by *n* for "newborn") and three stages for "adults" (yearlings, Stages 4 - 6 followed by *a* for "adult"). Note the classification of newborns (Stages 1*n*-E, 2*n*-M and 3*n*-L) and "adults" (Stages 4*a*-E, 5*a*-M and 6*a*-L) by time of season for births (E = early, M = mid-season, L = late). "Adult" stages are present only for purposes of accounting (e.g., contribution to stable stage distribution). The reproductive arcs from the newborn nodes have accounted for their fertilities.

Table 4. Parameter values for the component terms (P_i, B_i and m_i) in a matrix population model of water voles (*Microtus richardsoni*).

Parameter	Numeric value	Interpretation
m_E	6	Number of offspring produced early in season by "adults"
m_M	5	Number of offspring produced in mid-season by "adults"
m_L	4	Number of offspring produced late in season by "adults"
m_J	2	Number of offspring produced by young of the year
P_1	0.15	Annual survival of early newborns
P_2	0.1	Annual survival of mid-season newborns
P_3	0.075	Annual survival of late newborns
B_M	0.4	Probability of having a second (mid-season) litter
B_L	0.15	Probability of having a third (late) litter
B_J	0.1	Probability of having a litter in the season of birth

Table 5. The input matrix of vital rates, A (with cells a_{ij}), corresponding to the life cycle graph for water voles (*Microtus richardsoni*) shown in **Figure 12**. Newborns (Stages 1*n-E*, 2*n-M* and 3*n-L*) and "adults" (Stages 4*a-E*, 5*a-M* and 6*a-L*) are distinguished as to time of season for births (E = early, M = mid-season, L = late). Note that "adult" stages are present only for purposes of accounting (e.g., contribution to stable stage distribution). An additional feature is the subsuming of reproduction by young of the year into the fertilities of their parents (i.e., the cells in Row 2 include production of grandchildren as well as direct offspring).

Symbolic values

Stage	1	2	3	4	5	6
1	$P_1 mE$	$P_2 m_E$	$P_3 m_E$	0	0	0
2	$P_1*B_M*m_M+ P_1*m_E B_J*m_J$	$P_2*B_M*m_M+ P2*m_E*B_J*m_J$	$P_3*B_M*m_M+ P_3*m_E B_J*m_J$	0	0	0
3	$P_1*B_M*B_L*m_L$	$P_2*B_M*B_L*m_L$	$P_3*B_M*B_L*m_L$	0	0	0
4	$P_1(1-B_M)(1-B_L)$	$P_2(1-B_M)(1-B_L)$	$P_3(1-B_M)(1-B_L)$	0	0	0
5	$P_1*B_M(1-B_L)$	$P_2*B_M(1-B_L)$	$P_3*B_M(1-B_L)$	0	0	0
6	$P_1*B_M*B_L*m_L$	$P_2*B_M*B_L*m_L$	$P_3*B_M*B_L*m_L$	0	0	0

Numeric values

Stage	1	2	3	4	5	6
1	0.9	0.6	0.45	0	0	0
2	0.48	0.32	0.24	0	0	0
3	0.036	0.024	0.018	0	0	0
4	0.0765	0.051	0.03825	0	0	0
5	0.051	0.034	0.0255	0	0	0
6	0.009	0.006	0.0045	0	0	0

Table 6. Possible sensitivities only matrix, S (remainder of matrix consists of zeros), for a matrix population model of water voles (*Microtus richardsoni*). The three transitions to which the λ of water voles is most sensitive are: early reproduction by early newborns (Cells s_{11} = 0.727), mid-season reproduction of early newborns (s_{21} = 0.485), and early reproduction of middle newborns (s_{12} = 0.388).

Stage	1	2	3
1	0.727	0.388	0.029
2	0.485	0.258	0.019
3	0.363	0.194	0.015

Table 7. Elasticity matrix, E (remainder of matrix consists of zeros), for a matrix population model of water voles (*Microtus richardsoni*). The λ of water voles is most elastic to changes in early reproduction by early newborns (e_{11} = 0.528), followed by equal values for mid-season reproduction by early newborns (e_{21} = 0.188) and early season reproduction by mid-season newborns (e_{12} = 0.188).

Stage	1	2	3
1	0.528	0.188	0.011
2	0.188	0.067	0.004
3	0.011	0.004	0.0002

have the useful property of summing to 1.0. The λ of water voles is the most elastic to changes in early reproduction by early newborns (Node 1 back to Node 1; 0.528 = 53 percent), followed by mid-season reproduction of early newborns (from Node 1 to Node 2; 0.188 = 19 percent), equaled by early reproduction of middle newborns (Node 2 back to Node 1; 0.188 = 19 percent). The sensitivities and elasticities for water voles correspond exactly in the relative magnitude of the three most important transitions. These are the data pieces that should be most carefully monitored to refine life cycle analysis.

Partial derivatives can be used to calculate the partial sensitivity and elasticity of λ to changes in component input terms (Caswell 2000). Such partial analyses are particularly useful in the case of the present model because only the fertility transitions (the nine cells in the upper left of the original matrix) have non-zero sensitivities or elasticities. That is because the "adult" nodes have no outflow – no links to later stages or back to newborns. Nevertheless, the transitions with non-zero sensitivities and elasticities include component terms (P_i, B_i, and m_i) related to the three kinds of vital rate elements (survival, probability of additional breeding events, and fertility). Partial sensitivity results indicate the absolute changes in the P_i (survival rates) will have the greatest impact on λ. Changes in probability of additional breeding events (B_i) will have less effect, and changes in fertility (m_i) will have the least impact on λ. The percent of total partial sensitivity accounted for by P_i terms is 81.5, with 16.1 percent

accounted for by B_i terms, and 2.4 percent by m_i terms. The P_i term alone accounts for 52 percent of the total partial sensitivities. Partial elasticity results indicate that proportional changes in m_i (fertilities) will have the greatest impact on λ (49.1 percent of the total partial elasticity), and changes in the probability of additional breeding events (B_i) will have the least impact on λ (4.7 percent of the total partial elasticity). Again, the P_i term accounts for a large proportion (37 percent) of the total partial elasticities.

The difference between sensitivity and elasticity conclusions results from the weighting of the elasticities by the value of the original arc coefficients (the a_{ij} cells of the projection matrix). Because the F_i (fertility transitions) have large values (F_{11} = 0.09), ten times larger than any G_i transition describing transitions among stages, such as the arc from Node 1 to Node 4), the m_i contribution will include terms of large magnitude that "inflate" the corresponding elasticities. Management conclusions will depend on whether changes in vital rates are likely to be absolute (guided by sensitivities) or proportional (guided by elasticities).

At the time of the annual census (near the end of the breeding season), three sizes of young of the year should represent 91.2 percent of the population, and the remaining 8.8 percent consist of three female adult categories, those that produced one, two, or three litters (**Table 8**). Reproductive values (left eigenvector) for the three categories of adult females were 1.000, 0.667, and 0.500. That is, mid-season newborns (Stage 2) were

Table 8. Stable age distribution (right eigenvector) from a matrix population model of water voles (*Microtus richardsoni*). At model census, 91.2 percent of the individuals in the population were 3 categories of newborns. The remaining 8.8 percent of individuals were distributed across 3 categories of adults; those that produce 1 litter, those that produce 2 litters, and a relative few that produce 3 litters.

Stage	Description	Proportion
1	Newborn (early season)	0.580
2	Newborn (mid-season)	0.309
3	Newborn (late season)	0.023
4	Adult (one litter)	0.049
5	Adult (two litters)	0.033
6	Adult (three litters)	0.006

valued at two thirds and late season newborns (Stage 3) were valued at half of the value assigned to those born earliest in the breeding season.

Cochran and Ellner (1992) derived a method for assessing the total lifetime output of offspring (R_o) by each of the different types of newborns. These offspring outputs are weighted by the reproductive values of the various newborn types to yield an estimate of "newborn equivalents". An individual producing a late season newborn is credited "half a newborn" and a mid-season mother gets credit for only "two thirds of a newborn". Early newborns were estimated to produce a lifetime total of 1.238 newborn equivalents per female, mid-season newborns were estimated to produce a lifetime total of 0.825 newborn equivalents and late season newborns were estimated to produce a lifetime total of 0.619 newborn equivalents.

Partial sensitivities, particularly the contribution of survival rates, partial elasticities, reproductive values, and R_o all emphasize the importance of early and mid-season newborns and their survival rates to population growth. The survival rates of these two stages represented 52 percent (P_1) and 28 percent (P_2) respectively of the summed partial sensitivities of λ to changes in the component terms (P_i, B_i, and m_i) of the vital rates. The partial elasticity analysis also pointed to an important influence of P_i (37 percent of summed partial elasticities) with early reproduction by early newborns even more important (m_E accounted for 42 percent of the summed partial elasticities). In the partial elasticity analysis, the single most important component term was m_E, the number of early season offspring produced. This term accounted for 42 percent of the summed partial elasticities, followed in importance by P_1 (37 percent) and P_2 (9 percent).

Summary

In summary, this matrix population analysis suggests that water vole populations depend largely on the number and survival of early and mid-season newborns. It follows that actions that degrade habitat in the early and middle portions of the breeding season are likely to have disproportionately large effects on population growth. Survival of newborn water voles depends upon nest security within subterranean burrows (Ludwig 1981). Maintenance of the stream bank soil structure in which these burrows are excavated is therefore essential to nest security and the survival of newborns. In both the Beartooth Mountains and the Big Horn Mountains, the first litter of pups is born in late June or early July (Klaus et al. 1999, Klaus 2003). As mentioned earlier, stream banks are most susceptible to compaction by large grazing mammals early in the spring and summer when the soil is moist. Clearly, managers should evaluate the timing of livestock access and other soil- and vegetation-disturbing activities along alpine and subalpine streams in order to maintain stream bank soil structure, burrow integrity, and nest security for water voles in June and July.

Limits to population growth

Ideally, a discussion of limits to population growth would identify specific and discrete habitat components (e.g., food plants, structures providing protection to natal burrows) whose abundance and distribution drive the abundance and distribution of the target population. However, we simply do not yet know enough about water vole life history and ecology to draw such ultimate conclusions, and instead we are required to discuss more proximate limiting factors.

Water voles are adapted to a rather rare and fragmented habitat in Region 2; namely, moist alpine or subalpine meadows of willows, graminoids, and forbs atop deep soils and adjacent to low-gradient stream segments. The extent and connectivity of such habitat is clearly an overarching constraint on water vole populations. Given the general characteristics of high-elevation riparian habitats in the Rocky Mountains, it seems reasonable to assume that deep soil with a texture that supports and maintains burrows may be the most limited of these habitat components. However, we again caution that more study is needed to understand ultimate factors limiting water vole populations.

Superimposed upon this naturally fragmented habitat are several conditions that are pervasive enough in both time and space to be considered limiting factors. The simple harshness (e.g., short growing season, low temperatures, heavy snowpack) of the alpine and subalpine climate likely suppresses water vole populations below levels that they could maintain in milder regions. Similarly, drought, which is usually considered episodic but occurs with enough frequency in the Central Rocky Mountains to be considered a regular event, probably reduces water vole distribution and abundance relative to similar habitat in more consistently-moist areas (see Klaus et al. 1999).

Heavy grazing of riparian meadows by livestock, native ungulates (e.g., *Cervus elaphus*), or both groups is rather widespread and common in both the Shoshone and Bighorn National Forests, and can reduce the quality of water vole habitat and water vole abundance (Clark and Stromberg 1987, Luce 1995, Klaus et al. 1999, Klaus 2003). Large grazers compact soil, which collapses existing burrows and possibly precludes construction of new ones, and they also reduce protective cover by removing substantial amounts of vegetation. Heavy grazing may also reduce the quality of winter habitat for water voles because vegetation can suspend the snowpack and create a larger subnivean space. In the Shoshone National Forest, heavy grazing that noticeably affected soils and vegetation precluded water voles from occupying a site, while light to moderate grazing was suspected to reduce water vole population density and viability (Luce 1995). In some areas dense stands of willows appeared to minimize livestock use of streamside sites, and water voles were captured in these more protected areas (Klaus 2003).

Fragmented habitat, consistently harsh climate, regular drought, and persistent heavy grazing probably combine synergistically to limit water vole populations to lower levels than would any one factor alone.

The interactions and relative effects of these factors on water voles have not been directly studied. It is important to note that while factors that limit water vole populations are important on both the Shoshone and Bighorn National Forests, they may be of most critical importance on the latter. Because of their extreme rarity and geographic isolation on the Bighorn National Forest, water voles appear to be at greater risk of extinction on the Bighorn National Forest than on the Shoshone National Forest where they are more abundant, widespread, and connected to other regional centers of occurrence.

Community ecology

Predators

Predation on water voles is rarely documented, but in the Shoshone National Forest, coyote (*Canis latrans*), red fox (*Vulpes vulpes*), grizzly bear (*Ursus arctos*), and long-tailed weasel (*Mustela frenata*) have been observed at water vole burrows (M. Klaus unpublished data). Owl feathers have been found near burrow entrances (Pattie 1967). Ludwig (1981) observed American marten within water vole colonies and found a water vole radio collar in the nest of a short-tailed weasel (*Mustela erminea*). Goshawk (*Accipiter gentiles*), a variety of owls, striped skunk (*Mephitis mephitis*), and the least weasel (*Mustela nivalis*) may also prey upon water voles (Ludwig 1981). Based on range overlap and habitat preferences, occasional predation by mink (*Mustela vison*) and northern river otter (*Lontra canadensis*) is likely. Clearly, more direct research is necessary to determine if predation is a major mortality factor.

Competitors

There have been almost no studies regarding competitors of, or effects of competition on, water voles. In the northern Rocky Mountains and the Cascade Mountains water voles occur near mountain streams, whereas montane voles are usually trapped in valleys or meadows away from the side of the stream (Anderson et al. 1976). In the Shoshone National Forest, once a water vole colony was identified, the only other small mammal trapped within the colony was the insectivorous northern water shrew (*Sorex palustris*). In the Bighorn National Forest such exclusive water vole colonies were not observed; western jumping mice (*Zapus princeps*), northern water shrews, montane voles, and other small mammals were captured alongside water voles (**Table 9**). In Alberta, water voles were captured within their habitat more

Table 9. Abundance of small mammals captured at sites occupied by water voles (*Microtus richardsoni*) in the Bighorn National Forest, Wyoming. From Klaus 2003. Cell values are number of individuals.

Site	*Microtus richardsoni*	*Clethrionomys gapperi*	*Microtus montanus*	*Mustela erminea*	*Peromyscus maniculatis*	*Sorex palustris*	*Tamius minimus*	*Zapus princeps*
Bald Mountain Creek (2743 m)	22		21			16		73
Dome Lake (2663 m)	3			1		1		1
Duncum Creek (2572 m)	4	2						5
Fool Creek (2484 m)	6		32		3	27		10
Fool Creek Exclosure (2484 m)	7		42		12	14	3	21
Rooster Hill Exclosure (2798 m)	5					1		4
Wilderness Creek (2719 m)	5	1	1			1	1	
Wyoming Gulch (2804 m)	3	3	21		2	10		2
Total	55	6	117	1	17	70	4	116

frequently than other species, but *M. longicaudus*, *M. pennyslvanicus*, *Clethrionomys gapperi*, *Synaptomys borealis*, *Peromyscus maniculatus*, *Zapus princeps*, *Spermophilus columbianus*, *Eutamias amoenus*, *Sorex palustris*, *S. cinereus* and *Microsorex hoyi* were occasionally captured (Ludwig 1981, 1999). As stated above for predation, more direct research is needed to evaluate the effects of competition on water voles.

Parasites and disease

Bacteria, arthropods, and helminthes have been found on or in water voles. Ludwig (1984a) lists nine species of flea and four species of mite as the major ectoparasites of water voles. Only one endoparasite, a cestode, has been reported (Ludwig 1984a), even though more probably exist.

Little is known about water vole diseases. Pattie (1967) captured water voles with a disease similar to "big foot", and beta-hemolytic streptococci were isolated from these individuals. Ludwig (1981) reported bacterial hepatitis in one water vole.

Symbiotic and mutualistic interactions

Herbivores commonly have symbiotic interactions with microbes that ferment polymers, like cellulose, which cannot be digested by the animal. Three distinct zones are present in the stomach of *Microtus*: the forestomach, an area of glandular mucosa, and the pylorus. In the forestomach, rod-shaped bacteria are attached perpendicularly, which suggests a symbiotic association between the bacteria and *Microtus* (Philips 1985).

Envirogram

The web of ecological relationships for water voles is depicted in **Figure 13**, an envirogram following Andrewartha and Birch (1984). This is a representation of the proximal and distal factors thought to affect water vole distribution and abundance. The relative importance of these factors is not represented.

CONSERVATION

It is difficult to confidently discuss the conservation of any taxon for which there is a decidedly limited amount of scientific information. Nevertheless, our state of knowledge of the water vole clearly identifies some potentially important conservation issues, and at least hints at several others. This discussion is intended as a synthesis of all information presented to this point in this document, and it is intended to be largely referenced to that information.

Our current knowledge of the status and ecology of water voles suggests that the persistence of the species in USDA Forest Service Region 2 may be threatened by multiple interacting factors. These threats can be roughly grouped into two categories: (1) natural

WEB			CENTRUM
3	2	1	

RESOURCES

weather ——————— water ————— vegetation ————— FOOD
parent material ——— soil ——┘

weather ——————— snow, rain —— WATER
soil ——————— bank structure ———— stream depth —┘
nutrient,
daily transportation,
dispersal

weather ———┐ water depth—— escape cover ——┐
             burrows   PREDATORS
             shrubs   alternate food —┘
soil ———————┘ other vegetation ——┘

weather ————— snow cover —┐
water ——┐ shrubs ——┘   THERMAL COVER
soil ———┘ herbaceous plants— nests
                             vegetation
          soil——————— burrows ——┘

bank structure ——— previous generations — burrows —┐
                   vegetation ——┘   REPRODUCTION
                   weather ——————— water —┘

prime habitat ——— COMPETITION
mates ——————— intraspecific

prime habitat ——————— interspecific

MALENTITIES
weather ——————— drought

big foot——┐
Streptococcus ——— disease
hepatitis ——┘

recreation————— trampling———— bank damage —— human-caused mortality
                              low water table —┘

large animal grazing —— trampling ————— bank damage —— grazer-caused mortality
                                        low water table —┘

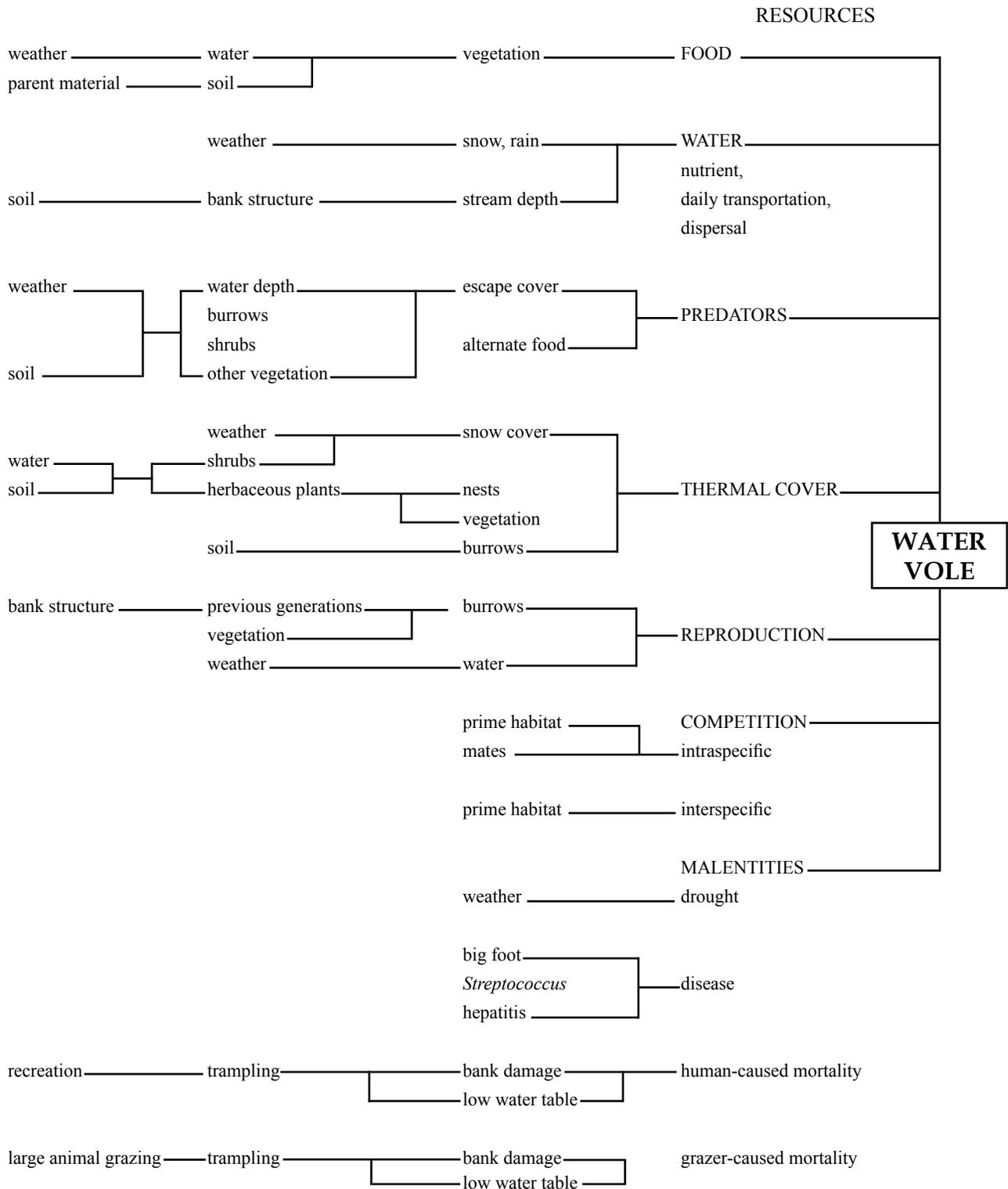**Figure 13.** Envirogram (after Andrewartha and Birch 1984) depicting the ecological interrelationships for the water vole (*Microtus richardsoni*).

WATER VOLE

threats stemming from the biogeographic history and intrinsic biology of water voles, and (2) anthropogenic threats stemming from management actions. Attempting to alleviate natural threats through management action would be very difficult and an impractical use of limited management resources. Natural threats are probably best viewed as a static context or "backdrop" that, although largely unalterable by management, will constrain the effectiveness of management actions.

Natural Threats

Biogeographic history

By virtue of post-Pleistocene changes in climate, which in turn altered the continental distribution of vegetation and associated faunas (see Beauvais 2000), water voles occupy only the two northernmost units (Shoshone and Bighorn National Forests) of Region 2 (**Figure 1** and **Figure 4**). Furthermore, because of their intrinsic requirement for alpine and subalpine conditions, water voles are almost completely restricted to national forests in this area. Within this already-limited range, water voles are further restricted to herbaceous riparian meadows and moist tundra. This limited distribution alone increases the probability of extirpation from Region 2.

The Shoshone National Forest supports a rather large and well-distributed amount of suitable habitat, and an apparently large number of water voles. Also, as discussed earlier, populations of water voles on the Shoshone National Forest exchange individuals with populations to the north, west, and south, which should provide beneficial genetic and demographic "supplements". Thus, from a strictly biogeographic perspective, water voles appear to be rather secure here.

In contrast, the Bighorn National Forest supports a rather small amount of habitat and relatively few water voles. Furthermore, the water vole population here has likely been completely isolated for the past several thousand years. This raises the possibility of reduced population viability due to reduced genetic variability (resulting from founder effect, genetic drift, and inbreeding), demographic imbalances, and, importantly, no immigration to alleviate such effects. In other words, Big Horn Mountain water voles may be at a heightened risk of entering the "extinction vortex" of Gilpin and Soule (1986; see also Caughley and Gunn 1996). The extinction vortex is a positive feedback cycle of detrimental population dynamics that eventually leads to extinction: when population size

is low, genetic variability and demographic stability decrease, which inhibits reproduction and survival that further reduces population size, and so on until the population is so small it is susceptible to final extinction through normal environmental stochasticity.

The likelihood of Big Horn Mountain water voles entering the extinction vortex is further raised by the highly fragmented distribution of suitable habitat here. The Big Horns sit in the rain shadow of the main chain of the Rocky Mountains, and yet they are not positioned far enough east to receive significant moisture from weather systems originating in the Gulf of Mexico. Therefore, this is a rather dry range with fewer permanent streams than mountains further to the west. Also, there are surprisingly few herbaceous riparian meadows within the small ring of boreal habitat on the Big Horns, and Big Horn Mountain tundra is notoriously dry and rocky. Thus, overland dispersal between adjacent watersheds probably involves longer distances of drier and more unsuitable habitat than in comparable areas of the Shoshone National Forest. Furthermore, the west slope of the Big Horn Mountains is so steep that most streams are deeply incised, leading to rather low habitat quality and almost no chance of water voles dispersing across upland divides. It is possible that water voles on the Big Horns are subdivided into many small and separate populations that exchange very few, if any, individuals with each other.

Because long-term geographic isolation is the primary driver of microevolution, water voles on the Bighorn National Forest could be significantly different from water voles elsewhere, possibly different enough to warrant unique subspecific status. Extinction from the Big Horn Mountains would therefore be a significant loss in regional biodiversity that could not be recouped through population re-establishment from distant stock.

Habitat specialization, fragmentation, and patchy populations

By virtue of their extreme specialization to high-elevation riparian meadows, water vole habitat in this region is naturally quite fragmented, leading to a patchy distribution at multiple scales. At a fine scale, small patches of suitable habitat occur infrequently along any given stream reach, and water vole population segments within those patches are connected via up- and downstream dispersal. At a coarser scale, water vole populations along individual stream reaches are connected to other stream reaches in the same headwater basin via streamside dispersal and infrequent overland dispersal. At a still coarser scale, water vole

populations in adjacent headwater basins exchange genes and individuals by overland dispersal through contiguous boreal habitat, but this exchange becomes limiting as the distance between watersheds increases (Klaus et al. 2001). When the hydrologic connection between adjacent basins occurs in dry sub-montane environments, such exchange is unlikely to occur. As headwater basins become more and more distant, their constituent water vole populations become more independent and therefore less likely to benefit from demographic and genetic input from each other. This is best exemplified by the likely complete separation of water vole populations on the Shoshone National Forest from those on the Bighorn National Forest, as well as the strong separation of water voles on Beartooth Pass from those at Togwotee Pass.

Probably few, if any, single patches of suitable habitat in Region 2 are large enough to support a self-sustaining population in the absence of immigration from other patches. In this context, water vole persistence in each of the Shoshone and Bighorn National Forests depends largely on successful inter-patch dispersal between local groups within the entire Forest-wide population. Because the probability of successful inter-patch dispersal declines with distance, management for the long-term persistence of water voles should focus on maintaining a well-distributed network of occupied patches of high-quality habitat, as well as maintaining natural dispersal between these patches. Unfortunately, there are too few data at this time to more rigorously define the parameters (e.g., number of patches, size of patches, inter-patch distance) of such a network.

Drought

Drought probably has a large negative effect on water voles, and it might be best defined as the major ecological crisis or "crunch" time for the species. Drought can directly impact the persistence of water vole populations by reducing the number, size, proximity, and productivity of occupied patches as well as reducing inter-patch dispersal. Marginal habitats (e.g., ephemeral drainages, spring fed streams, sub-irrigated meadows) that are suitable under normal conditions are likely unsuitable under drought. Similarly, lowered water tables probably constrict the zone of moist suitable habitat alongside permanent streams. Overland dispersal, which is likely infrequent even under good conditions, may be almost completely eliminated as uplands become increasingly dry.

Severe and prolonged drought may lead to extinction from entire headwater basins; alternatively,

it may restrict water voles to only the largest and most suitable patches in a given basin. Under the scenario of local extinction, recolonization from an adjacent basin is possible given a relatively short overland distance and a relatively long period of normal or wetter-than-normal conditions. Recolonization of all suitable habitat in a basin from only a few source patches would also probably require a relatively long time. Management strategies aimed at long-term persistence of water voles should recognize that persistence under severe drought is likely a major limit on population viability; ensuring survival under drought conditions may be the best management focus.

Conversely, periods of higher than normal precipitation benefit water vole populations by simultaneously increasing the amount of suitable habitat (e.g., flowing springs and ephemeral drainages, sub-irrigated meadows, widened riparian zones) and the reproductive output of both sub-adults and adults (Racey 1960, Klaus et al. 1999). It is likely that wet periods also facilitate inter-patch dispersal and colonization of small and distant patches of suitable habitat by not only increasing the number of dispersing individuals but also increasing the suitability of formerly dry uplands as dispersal routes. Wet periods may be "recharge" periods for water vole populations, where much suitable (and probably even marginal) habitat becomes occupied. Increased inter-basin immigration may alleviate local demographic and genetic deficiencies. However, in order for water vole populations to maximally benefit from wet conditions they need to be already composed of a well-distributed network of occupied patches from which individuals can disperse to a majority of patches of suitable habitat.

Anthropogenic Threats

Livestock grazing

Heavy grazing by large mammals, whether native ungulates or livestock or a combination of both, can degrade the quality of water vole habitat through direct disturbance of soil and vegetation in riparian areas. Livestock grazing has been cited as likely the greatest anthropogenic threat to water voles in this region (Clark and Stromberg 1987, Friedlander 1995, Luce 1995). It is important to note that most of these conclusions are based on limited trapping information and observations of general habitat condition, and not on controlled experiments designed to specifically test the effect of livestock on water voles. The emphasis on livestock over free-ranging wildlife probably stems in part from the fact that livestock impacts are more

controllable by managers. Livestock grazing negatively impacts populations of small mammals in general, and populations of *Microtus* in particular (e.g., Eadie 1953, Getz 1970, Fleischner 1994). Livestock grazing also can shift the small mammal community away from high elevation riparian specialists like the water vole toward species that are habitat generalists (Grant et al. 1982).

The specific effect of livestock depends on the intensity and frequency of their grazing in the context of grazing by other large mammals. Infrequent livestock grazing with low stocking rates and long rotations may have little impact on water vole occupancy (Luce 1995, Klaus 2003), especially if native herbivores also use the area lightly. Higher grazing intensities of livestock, native herbivores, or both groups can reduce habitat quality by removing water vole food and cover and compacting soil, which can collapse existing burrows and prevent construction of new ones. Prolonged and intense livestock grazing, even in the absence of grazing by native species, can eliminate water vole habitat by destroying stream banks, widening stream channels, lowering local water tables, eroding soil, and altering nutrient cycling (Gifford and Hawkins 1978, Kauffman and Krueger 1984, Marcus et al. 1990, Armour et al. 1991, Platts 1991, Fleischner 1994, Belsky et al. 1999, Clary 1999). The negative effects of intense grazing may extend into the winter. For example, abundant erect vegetation helps suspend the snowpack and make the subnivean space more usable to voles (Birney et al. 1976); heavily grazed and trampled vegetation may not function in this manner.

Grazing by large mammals is probably most detrimental in early summer (June), when soils are wet and most susceptible to compaction, and water voles are producing their first litters of the season. The population matrix model discussed earlier (McDonald and Ise 2002) suggests that survival of, and subsequent reproduction by, water voles born in June probably have the largest effects on future population growth. Any disturbance to burrow security and maternal nutrition at this time could have disproportionately large effects on persistence and abundance within an occupied patch. Also, a burrow lost to trampling represents more than just a single lost reproductive attempt because multiple generations of water voles use the same burrows, and trampled soil is not likely to recover pre-compaction structure for a long time.

In general, livestock, some large native mammals such as elk, and water voles have similar preferences for low-gradient riparian zones dominated by moist herbaceous vegetation. In non-wilderness portions of the Shoshone and Bighorn National Forests, livestock grazing appears to be widespread and chronic, and may lower water vole abundance, survival, and reproduction within most patches of suitable habitat. Combined with drought, such pervasive impacts could contribute to local extinctions. In contrast, livestock grazing is generally less intense in designated Wilderness Areas on both national forests. In this context, wilderness areas may function as refugia within which water vole population segments have a higher probability of persistence through drought, and they may also function as population sources from which adjacent non-wilderness areas may be recolonized.

Other anthropogenic threats

Any action that degrades the quality of streams and streamside vegetation has at least some potential to degrade water vole habitat, but there is little research to support specific conclusions. Sediment load is likely to increase in watersheds experiencing construction of roads and trails, increased use of roads and trails, large fires, or timber harvest, but the effect of increased sedimentation on water voles has never been investigated. Similarly, Demboski (2001) felt that heavy recreational use may impact water voles at Crumarine Creek, Latah County, Idaho, but the impact of recreation on water vole site occupancy or abundance has also never been investigated. Fires may occasionally burn through riparian meadows, but the potential negative effects on water voles are not well understood and are likely to be short in duration. It is reasonable to assume that drastic changes to water quantity (e.g., major water withdrawals) or quality (e.g., heavy metal contamination from mine leachate) will have negative effects on water voles.

Water voles appear to flourish in discrete pockets of riparian habitat that meet their particular needs, despite the presence of potential competitors (**Table 9**). The impact of exotic species on water vole populations is not known. Introduced small mammals, such as house mice (*Mus musculus*, have not been reported from sites occupied by water voles, and are unlikely to reach high numbers in the harsh and remote habitats favored by water voles. Because water voles use a wide variety of plants for food and cover across their range, it seems unlikely that the presence of exotic plant species would have a direct negative impact on them. The possibility that long-term beaver (*Castor canadensis*) activity maintains a higher coverage of water vole habitat than would be realized in the absence of beaver is a topic of potentially fruitful research.

Conservation Status of Water Voles in Region 2

Our current knowledge of water voles suggests that they are at moderate-to-high risk of local extinctions throughout their range. The probability of local extinctions within Region 2 is increased simply because the species occupies a rather small area. Other contributing factors, detailed in the previous section, include (1) highly specialized habitat requirements in harsh, high-elevation environments, (2) naturally fragmented habitat leading to patchy populations of loosely-connected population segments, (3) a high susceptibility to episodic drought, which is a regular occurrence in Region 2, and (4) a high susceptibility to grazing by livestock and other large mammals, which is a widespread and persistent activity in much of Region 2. Because of their geographic isolation at a regional scale, water voles on the Bighorn National Forest may be especially prone to decline and local extinction. Furthermore, because of their possible intra-species uniqueness, declines or local extinctions of water voles on the Bighorn National Forest may have especially severe consequences to regional biological diversity.

However, it is important to recognize that water voles in Region 2 have persisted through periods in the past when some negative impacts may have been greater in both distribution and intensity. In the early-to mid-1900's livestock use was much heavier than at present throughout the Rocky Mountains, including the Shoshone and Bighorn National Forests. Designated Wilderness Areas were non-existent, and livestock were allowed to graze in high numbers in essentially all habitat types, including riparian areas in the subalpine and alpine zones. Habitat conditions for water voles should have been rather poor during this time, especially during the many droughts known from this period, and yet water voles persisted and now occupy a broad distribution that, at a coarse-scale, matches that of apparently suitable habitat.

A complete analysis of habitat conditions during the early- to mid-1900's, which is beyond the scope of this assessment, would need to account for substantially fewer native ungulates, a much less extensive road network, and other factors that could have promoted water vole persistence then. However, it is reasonable to assume that water vole populations have some resiliency to heavy livestock grazing and drought given a large enough area over which source populations can persist.

Data on population trends are essentially unavailable for water voles; this probably is the largest gap in our knowledge relative to conservation status of the species. In the Shoshone National Forest, one location (**Figure 8**) has maintained stable female fecundity estimates and stable, possibly even increasing, abundance estimates for thirty years (Pattie 1967, Klaus 1997). Baseline data are not available for any location in the Bighorn National Forest, but capture success was lower at all locations trapped in the Bighorn National Forest than at any trapped site in the Shoshone National Forest (Klaus et al. 1999, Klaus 2003). In general, the Bighorn National Forest appears to support fewer total water voles and fewer water voles per unit of suitable habitat, than does the Shoshone National Forest. Unfortunately, it is difficult to know exactly how much of the available Bighorn National Forest habitat is currently occupied by water voles since obvious signs of their activities are absent. In the Bighorn National Forest, capture was the only way to confirm habitat occupancy, and trapping is very labor intensive.

Because water voles are rarely studied, the extent that similar problems exist throughout the species' range is not known. We are aware of no on-going studies of water voles within Region 2 or any other location. Status rankings of water voles from some entities indicate a general assumption that the species is abundant and secure in most of its range. However, the lack of published research coupled with the difficulty of obtaining field data on distribution, abundance, and population trends suggests that most of these status estimates are conjectural.

Management of Water Voles in Region 2

Management of water voles in Region 2 should proceed from a basic understanding of the natural threats faced by the species, and the recognition that many of these threats cannot be influenced by management action. A high degree of specialization to a naturally fragmented riparian habitat type at high elevations constrains water voles into forming patchy, rather than contiguous, populations. Management strategies aimed at ensuring water vole persistence in a given landscape should therefore focus on maintaining a well-distributed network of occupied patches of high-quality habitat, and also on maintaining dispersal between those patches.

Furthermore, water voles probably suffer population declines during drought, and therefore

patches of suitable habitat intended to support long-term viability should ideally be sufficiently large and have a reliable water source to maintain water vole occupancy through prolonged dry periods. Whereas water vole distribution and abundance may be relatively high during years of above-normal precipitation, it is reasonable to assume that their distribution and abundance during dry periods will ultimately determine population viability. As a result, management strategies should be explicitly based on "worst case" environmental conditions during drought.

Based on our current knowledge of water vole life history, the most important anthropogenic impact on water voles in Region 2 is probably heavy grazing by livestock. In contrast to most natural constraints on population viability, the intensity and frequency of livestock grazing can be deliberately managed and thus likely represents the most efficient and effective way for managers to influence water voles in Region 2. Because suitable water vole habitat in designated Wilderness Areas usually receives little livestock grazing, such habitat may act as both a population refugium and population source. Although both the Shoshone and Bighorn National Forests support large tracts of designated Wilderness Areas, there are significant portions of non-wilderness on both units that are distant from and not hydrologically connected to potential Wilderness refugia/sources.

Tools and practices

Water voles have typically been studied by trapping (Pattie 1967, Anderson et al. 1976, Ludwig 1981, Klaus 1997), which is invasive and labor intensive but nonetheless is the best way to confirm site occupancy, especially in the absence of obvious latrines or runways (Klaus 2003). Water voles can be captured in large Sherman traps baited with a mixture of oats and peanut butter and set flush to the ground along alpine or subalpine streams in runways, by latrines, or by burrow entrances. If occupancy signs are absent, as in the Bighorn National Forest, traps can be placed along streams that meet general water vole habitat requirements. Traps should be checked at least twice a day, once early in the morning when most captures occur, and again late in the afternoon or early evening. Live trapping should be conducted according to the American Society of Mammalogists guidelines (Animal Care and Use Committee 1988). Some water vole trapping surveys are planned for the western slope of the Big Horn Mountains in summer 2002 (Allison personal communication 2002); some trapping may also occur within the Tongue River basin on the

Bighorn National Forest in summer 2002 (Golden personal communication 2002). We are unaware of any trapping efforts planned on the Shoshone National Forest (Barker personal communication 2002, Oakleaf personal communication 2002).

In both the Bighorn and Shoshone National Forests the best time to monitor water vole populations is from the middle of July to the end of September. Prior to the middle of July, population density is quite low, capture or observation requires extensive effort, and successes are few (M. Klaus, personal observation). In the Shoshone National Forest, observation of water voles and their signs is possible by walking along streams that meet their habitat requirements and where they have been captured in the past. Unfortunately, in the Bighorn National Forest, trapping is the only way to be certain of their presence. As discussed in more detail below under "Information Needs", managers may want to consider a monitoring program focused on presence/absence of water voles in a suite of patches of suitable habitat rather than a more traditional monitoring approach focused on abundance.

Maps of potential distribution and suitable habitat are important management tools for most vertebrates, but for water voles they may be especially critical. In general, knowing the amount and spatial arrangement of suitable habitat is crucial for the management of habitat specialists. In cooperation with Region 2, WYNDD has produced spatially explicit, predictive range maps covering all five states in Region 2 for several vertebrates of management concern, including water voles. Details and results of the water vole mapping effort are in Beauvais et al. (2003), and described briefly above under "Management Status and Natural History - Biology and Ecology - Distribution".

Importantly, as with all predictive range maps, the map in **Figure 1** should not be used to inform conclusions at spatial scales much finer than that at which the map was constructed. This particular map was constructed to show regional and statewide patterns in distribution, and therefore probably performs poorly at predicting distribution at scales much finer than the average Ranger District. Fine-scale maps of suitable habitat, which can be of great use to managers, require more intensive mapping techniques and finer-scale habitat data.

In the Bighorn National Forest, the fine-scale distribution of water vole habitat has been mapped for the Tongue River watershed based on stream gradient, size, and proximity to conifer stands. Suitable

habitat was delineated as a subset of potential habitat based on qualitative knowledge of current bank and vegetative cover characteristics. This information will be field verified (Golden personal communication 2002). Although this map will inform Forest Planning efforts, its qualitative and subjective nature reduces its effectiveness for long-term monitoring and trend analysis and reduces its applicability to other sites in the region. A more effective approach to fine-scale habitat mapping would use a more quantitative system of riparian habitat classification, of which there are several in existence.

The Bighorn National Forest currently uses stubble height to indicate grazing intensity on riparian areas, but stubble height alone is not a good indicator of water vole site occupancy. In the Shoshone National Forest, water voles occupy high elevation sites where vegetation height is below the Bighorn National Forest stubble height recommendation. Better information on the specific habitat features required by water voles, and how those features are influenced by grazing, drought, and other perturbations, are clearly needed (see "Information Needs" below).

We are unaware of any management actions specific to water voles or water vole habitat that have been implemented anywhere within the species' range, so it is not possible to report on the success of deliberate manipulations.

Information Needs

As with most poorly-studied taxa, basic field research into current distribution and habitat use is probably most urgently needed to inform management and conservation of water voles. Field surveys of poorly-sampled and unsampled areas will, relatively quickly, substantially increase our knowledge of water vole distribution and general habitat preferences on each national forest. We strongly urge that any such survey efforts use a quantitative and replicable system of riparian habitat classification to describe all surveyed sites; this will help build a data set from which habitat preferences and fine-scale maps of habitat distribution can be derived.

Beyond basic field inventories, annual monitoring that could reliably estimate population trends by basin, by USFS National Forest, and statewide would be extremely valuable. However, the amount of data required for such estimates may be prohibitively expensive to collect because water voles are difficult to study and occur in some of the most remote areas

of Region 2. Although less useful than annual, Region-wide estimates of abundance, it may be more practical to pursue a two-level monitoring strategy: (1) annually monitor the presence/absence of water voles in a large and well-distributed subset of patches of suitable habitat on both the Shoshone and Bighorn National Forests, and (2) annually monitor the abundance of water voles within only a few, select populations. At the very least, this would produce annual estimates of the ratio of occupied patches to unoccupied patches, which would inform managers as to the general status of water vole populations. Of course, pilot studies are necessary to estimate variation in the target statistic in order to properly design (e.g., estimate necessary sampling effort) a monitoring program of any type. Because of the geographic separation of water voles on the Shoshone and Bighorn National Forests, and because of the ecological differences between these two management units, pilot studies and resulting monitoring programs may need to be conducted independently on each national forest.

Water vole populations are obviously patchy at several scales, and the synthesis of current knowledge provided in this assessment suggests that long-term persistence in any given patch depends not only on habitat quality and disturbance within that patch but also on the occasional importation of individuals from nearby patches. Thus long-term management of water vole populations needs to be informed by estimates of dispersal distances, likelihoods, and frequencies across a range of habitat configurations; i.e., what are the habitat parameters (e.g., size of patches, distance between patches, quality of patches, quality of inter-patch habitat) that define a connected network of water vole subpopulations? There is a rather deep literature base from the fields of island biogeography and metapopulation biology that will serve as a solid foundation for researchers designing studies to address these issues for water voles.

There are many questions regarding the specific impacts of drought and livestock grazing on water voles and water vole habitat. Obviously, the most usable information in this context is not whether drought or livestock grazing is generally positive or negative, but rather the quantitative relationships between intensity, duration, and frequency of these perturbations and water vole survival and reproduction. Importantly, it is reasonable to assume that water voles do not respond directly to grazing and drought, but instead respond to the changes in vegetation and soil structure brought about by these processes. Therefore, a complete model of water vole habitat use needs to quantify the responses

of survival and reproduction to vegetation and soil structure, then further relate vegetation and soils to grazing and drought. Such quantitative information does not exist now, forcing managers to rely on poor substitutes such as qualitative habitat assessments and stubble height measurements.

Several genetic and taxonomic questions about water voles need to be investigated in Region 2. An issue of obvious importance is the extent to which Big Horn Mountain water voles are unique from water voles on the main chain of the Rocky Mountains. Geographically isolated populations can represent unique evolutionary units that contribute substantially to regional biodiversity, a fact that is recognized in statute by the provision of the U.S. Endangered Species Act that extends to distinct population segments (Pennock

and Dimmick 1997). Taxonomic uniqueness could be investigated by a variety of genetic and morphological comparisons. Because each technique has different strengths and weaknesses, a "weight of evidence" approach based on multiple independent assessments may be the best research strategy here.

Water voles share general habitat requirements with other species of management concern in Region 2, such as Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*), Hapeman's sullivantia (*Sullivantia hapemanii* var. *hapemanii*), and northern blackberry (*Rubus acaulis*). Coupled with the high ecological value of riparian areas in general, this raises the possibility of implementing a multi-species strategy for more efficient and effective management of riparian resources in this area.

DEFINITIONS

Allozyme – allelic form of a protein or enzyme that can be distinguished by electrophoresis.

Alpine – of or pertaining to areas at very high elevations, generally above upper tree line.

Boreal – of or pertaining to northern subarctic regions or the equivalent high-elevation life zones; see Taiga.

Clade – a group of organisms defined by exclusive characteristics.

Dispersal – movement away from the natal site, particularly by juveniles.

Fitness – nonrandom reproduction resulting in differential representation of genotypes over several generations.

Fixation index (FST) – the loss of heterozygosity due to genetic drift of an isolated subpopulation where $F_{ST} = 0$ implies no inbreeding and $F_{ST} = 1$ implies complete inbreeding.

Gene flow – genetic exchange between different populations of one species.

Genetic distance – a number computed as the number of nucleotide substitutions per site.

Genetic drift – changes in allele frequency from one generation to the next based due to chance fluctuations.

Haplotypes – specific combinations of linked alleles in a cluster of related genes.

Heterozygous – a genotype where the two copies of the gene that determines a particular trait are different.

Induced ovulation – release of ova from the ovary as a result of sexual stimulation.

Irrupt – a large and rapid increase in population size.

Metapopulation – a patchy population made of small, local sub-populations that exchange immigrating/emigrating individuals. The dynamics of each sub-population are asynchronous, and sub-populations may periodically go extinct and then become re-established via colonization from other subpopulations.

Phylogenetic – referring to the historical and evolutionary relationship between organisms.

Refugia – pockets of habitat where individuals may persist under harsh conditions, and subsequently re-populate nearby areas.

Relict – a remnant of a formerly larger entity, such as a small and isolated population that remains from the contraction of a formerly large and widespread population.

Subnivean – beneath the snow.

Sympatry – two different but related taxa found in the same place.

Taiga – northern boreal forests, typically of small conifers whose crowns remain separated.

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