Dispersal of Microtus richardsoni in the Beartooth Mountains of Montana and Wyoming
by Marion Klaus

A thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Biological Sciences
Montana State University

Abstract:
The purpose of this study was to determine if Microtus richardsoni, the water vole, is geographically isolated within drainages or between four adjacent watersheds in the Beartooth Mountains of Montana and Wyoming. Water voles were named a sensitive species in the Rocky Mountain Region of the Forest Service, Region 2. Since local extinction is possible, their capacity to disperse becomes a question central to their management. Capture success, reproductive activity of males, the number of embryos found in trap-killed females, and the mean weight of Class I males (those weighing up to 49g) was significantly greater during the unusually wet summer of 1992 in comparison to the drier summers of 1990-91. In comparing water voles from grazed and nongrazed locations, capture success was significantly greater in ungrazed drainages and the mean weight of Class I females (those weighing up to 49g) was significantly greater in grazed than in ungrazed drainages. A relationship between an increase in population of water voles and precipitation is suggested by the data. Confirmation of any relationship between grazing of domestic livestock and impacts on water voles should be sought in other studies. Nuclear DNA obtained by nondestructive sampling of individuals representing each trapping location was examined at 31 enzyme or protein loci. Only ADH, EST-1 and SOD-1 were polymorphic. ADH and EST-1 were in Hardy Weinberg Equilibrium, but SOD-1 was not. Mitochondrial DNA, obtained from nondestructive sampling, was found to be polymorphic with 9 different restriction enzymes. The size of the fragments produced by each restriction enzyme was estimated and ordered into a site map. A total of 51 sites were found with the 9 restriction enzymes. This resulted in 29 different haplotypes from 142 individuals. Analysis of the allozyme and mitochondrial DNA variation suggests that the water voles are capable of dispersing across the four watersheds studied in the Beartooth Mountains, but that they are isolated from water voles found 150 km away at Togwotee Pass in the Absaroka Mountains of Wyoming. Their ability to disperse overland is also suggested by these data.

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APPROVAL

of a thesis submitted by

Marion Klaus

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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Dr. Ernest R. Vyse — E R Vyse (Signature) — 4/14/97 Date

Approved for the College of Graduate Studies

Dr. Robert L. Brown — R L Brown (Signature) — 4/18/97 Date

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ABSTRACT

The purpose of this study was to determine if *Microtus richardsoni*, the water vole, is geographically isolated within drainages or between four adjacent watersheds in the Beartooth Mountains of Montana and Wyoming. Water voles were named a sensitive species in the Rocky Mountain Region of the Forest Service, Region 2. Since local extinction is possible, their capacity to disperse becomes a question central to their management. Capture success, reproductive activity of males, the number of embryos found in trap-killed females, and the mean weight of Class I males (those weighing up to 49g) was significantly greater during the unusually wet summer of 1992 in comparison to the drier summers of 1990-91. In comparing water voles from grazed and nongrazed locations, capture success was significantly greater in ungrazed drainages and the mean weight of Class I females (those weighing up to 49g) was significantly greater in grazed than in ungrazed drainages. A relationship between an increase in population of water voles and precipitation is suggested by the data. Confirmation of any relationship between grazing of domestic livestock and impacts on water voles should be sought in other studies. Nuclear DNA obtained by nondestructive sampling of individuals representing each trapping location was examined at 31 enzyme or protein loci. Only ADH, EST-1 and SOD-1 were polymorphic. ADH and EST-1 were in Hardy Weinberg Equilibrium, but SOD-1 was not. Mitochondrial DNA, obtained from nondestructive sampling, was found to be polymorphic with 9 different restriction enzymes. The size of the fragments produced by each restriction enzyme was estimated and ordered into a site map. A total of 51 sites were found with the 9 restriction enzymes. This resulted in 29 different haplotypes from 142 individuals. Analysis of the allozyme and mitochondrial DNA variation suggests that the water voles are capable of dispersing across the four watersheds studied in the Beartooth Mountains, but that they are isolated from water voles found 150 km away at Togwotee Pass in the Absaroka Mountains of Wyoming. Their ability to disperse overland is also suggested by these data.

INTRODUCTION AND NATURAL HISTORY OF *MICROTUS RICHARDSONI*

Microtus richardsoni (De Kay), the water or Richardson's vole, is a rodent in the family Muridae and subfamily Arvicolinae that has been present in North America since the mid-Pleistocene (Anderson, 1985; Burns, 1982; Hoffmann and Koeppl, 1985). It occupies a highly disjunct range within mountainous areas of Montana, Wyoming, Utah, Idaho, Oregon, Washington, Alberta and British Columbia (Hall, 1981; Hoffmann and Koeppl, 1985). Of the four subspecies recognized throughout its range only *M. r. macropus* (Merriam) is found in Montana and Wyoming (Hoffmann and Koeppl, 1985). Except for muskrats, water voles are the largest arvicoline rodents within their geographic range (Ludwig, 1984).

Water voles are found infrequently. Of the 4,500 individual small mammals captured during a 6 year study in the western Cascade Mountains of Oregon, only 1% were water voles (Hooven, 1973). They are typically found in small populations of 8-40 animals that are distributed linearly along alpine streams (Anderson et. al., 1976; Clark and Stromberg, 1987; Hollister, 1912; Hooven, 1973; Ludwig, 1988; Pattie, 1967; and Racey and Cowan, 1935). Water voles breed during June, July and August (Anderson et. al., 1976; Ludwig, 1984). Estimates of mean water vole litter size are 6.0 (Negus and Findley, 1959), 5.45 (Pattie, 1967), 7.85 (Brown, 1977) and 5.52-6.11 (Ludwig, 1981). Voles are well known for their three-to-four year population cycles (Taitt and Krebs, 1985), yet only one anecdotal record exists of water vole population irruptions. Racey (1960) described water vole population booms at Alta Lake in the Pemberton Valley in British Columbia during the summers of 1927, 1949, and 1958. During each of these years, precipitation exceeded the mean (Simpson, et al, 1932; Strauss and Reichelderfer, 1959; Connor and White, 1965).

Water voles are relatively slow to mature. Only 6.2-11.3% of the young females and 5.9-20.0% of the young males reproduce in their first year (Ludwig, 1984). Of the overwintered adult females, 62.5% were pregnant while 20% produced two litters in one breeding season (Ludwig, 1981). The majority of water voles overwinter only once and 88.9% of overwintered adults disappeared by the end of September (Ludwig, 1984). Ludwig (1981) radio-tracked one female and estimated her lifespan to be 16 months.

Adult water voles are big and can be distinguished from other voles by their total length (212-260 mm), weight (85-120 g.), and hind foot length (25-30 mm) (Clark and Stromberg, 1987). Male water voles are larger than females. Young water voles are more difficult to distinguish from other sympatric species of voles, but *M. r. macropus* have large hind feet that can help identify them. The length of the hind foot was the most reliable characteristic for identifying young water voles in this study. One young water vole that weighed only 18 g had hind feet measuring 23.5 mm. By comparison, *Microtus montanus* has an adult hind foot length of 17-21mm (Clark and Stromberg, 1987). The number of plantar tubercules on the hindfoot was suggested as a way to distinguish *Microtus richardsoni* from other species (Ludwig, 1984), but this was not found to be a consistent feature. The number of tubercules varied between water voles and between the two hindfeet of one individual water vole.

Water voles were probably isolated in mountain ranges as they followed tundra-like vegetation into high elevations after the Pleistocene glaciations (Hoffmann and Koeppl, 1985). In Canada, they are found between 1,524 to 2,378 meters in elevation (Banfield, 1974) and between 914 to 3,201 meters in the United States (Ludwig, 1984). Water voles generally do not occur in isolated mountain ranges apart from the Cascades and northern Rocky Mountains. They are found in only two isolated mountain ranges in the northern great plains, the Big Belt mountains of Montana and the Bighorn mountains of Wyoming (Hoffmann and Jones, 1970). This suggests they are unable to disperse across lowland barriers to reach suitable subalpine or alpine habitat and have low colonization rates as well as high extinction rates. These characteristics are not unusual for montane mammals (Brown, 1971).

Water voles are nocturnal, semi-aquatic, and have highly specific riparian habitat requirements (Ludwig, 1981). Streams are used for escape and as transportation routes for daily movement and dispersal (Anderson et. al., 1976; Ludwig, 1981). Many of the smaller alpine streams used by these voles are ephemeral and dependent upon melting snow and precipitation for their existence. Water voles are found in linear colonies along alpine or subalpine streams with about 5° slope and narrow stream channels, a well-developed substratum of soil for burrowing next to the stream and mid-to-late seral stage stream-side vegetation consisting of willow, sedges, grasses and mesic forbs that provide

75% cover (Anderson et. al., 1976; Anthony, et. al., 1987; Blankenship, 1995; Getz, 1985; Ludwig, 1981; Pattie, 1967; Reichel, 1986). Preferred sites are often used by successive generations of water voles while similar habitat adjacent to a colony remains unoccupied (Ludwig, 1981). Preferred sites are well drained and have a deeply developed soil layer adjacent to the stream (Ludwig, 1981). During the summer, adults have a linear home range along a stream (Anderson, et. al., 1976; Pattie, 1967; Ludwig, 1981). Adult females stay within small, exclusive home areas while adult males move over longer portions of stream and overlap the seasonal ranges of adult females and adult males (Anderson et. al., 1976; Ludwig, 1981). The site loyalty and exclusive home range of adult females suggest that a stream-side home area with an underground nest site and adequate food are the keys to female reproductive success (Ludwig, 1981). The diet of water voles is known to include grasses, sedges, seeds, inner bark of willow twigs and forbs (Anderson et. al, 1976; Clark and Stromberg, 1987). The upper limit of water vole population size may be partially determined by the number of habitat sites available along streams.

Environmental assessments required for reallotment of grazing permits in the Rocky Mountain Region of the Forest Service, Region 2, now include consideration of the water vole (USDA-Forest Service, 1994). The water vole was recently placed on the Region 2 sensitive species list because it is rare to uncommon in this region, and it requires specific riparian habitat that is declining and may be damaged by poor grazing practices (Friedlander, 1995). Continuous heavy grazing can alter the characteristics of riparian habitat by widening the stream channel, compacting the soil, and moving the plant community to an earlier seral stage. These factors probably combine to make an area unsuitable for water voles (Blankenship, 1995; Clark and Stromberg, 1987). Because water voles are vulnerable to riparian changes, there is concern about the continued viability of water vole populations in the grazed areas of this region (Blankenship, 1995). The short alpine breeding season, narrow habitat range, and low population densities result in small populations that are not buffered against habitat degradation and local extinction. Since local extinction is a possibility, their capacity to disperse becomes a question central to their management as a sensitive species.

The purpose of this study was to determine if allozyme and mitochondrial DNA (mtDNA) variation suggest water voles are geographically isolated within drainages or between adjacent watersheds on the Beartooth Plateau of Montana and Wyoming.

Evidence concerning the capability of water voles to disperse is addressed by restriction fragment length polymorphism (RFLP) analysis of mtDNA with supporting evidence from allozyme analysis of nuclear DNA. Information from mtDNA can be used to study dispersal of females and population dynamics (Avise, 1986) while allozyme analysis of nuclear DNA can be used to study dispersal of both sexes. Dispersal can be reflected in the distribution of phenotypic frequencies (Birdsall, 1972). Avise et al. (1979a) compared mtDNA sequences and found heterogeneity within and among natural populations of three species of *Peromyscus*. This technique can be used to estimate relatedness of mitochondrial genomes, and because mtDNA is maternally inherited, it is possible to follow intra- and interdemic movements of females. Since mtDNA evolves rapidly in terms of nucleotide substitutions, it can be used to distinguish between closely related organisms (Brown et al., 1979; Li and Graur, 1991). Kessler and Avise (1985) demonstrated that mtDNA heterogeneity in a population of *Sigmodon hispidis* was sufficient to describe spatial and temporal use of habitat. The mtDNA phylogeny suggests historic relationships among haplotypes that are inferred from shared and presumably derived mutations (synapomorphies) in a cladistic analysis. Geographic distribution can be coupled with phylogeny to describe the phylogeographic pattern for a species (Avise, 1989).

DEMOGRAPHICS OF *MICROTUS RICHARDSONI* IN THE BEARTOOTH MOUNTAINS

Water voles use streams as corridors for dispersal to preferred patches of habitat, but the glaciated mountain topography between watersheds may restrict movement. A study site with these features was selected in the Beartooth Mountains and straddles the Montana and Wyoming border (Figure 1). This area consists of ten drainages or parts of drainages within four adjacent watersheds that comprise the headwaters of the Clarks Fork of the Yellowstone River. All are managed by the Shoshone National Forest's Clarks Fork District office in Region 2 of the USDA-Forest Service except for Quad Creek, which is managed by the Custer National Forest's Beartooth District in Region 1. Elevations of the drainages where water voles were trapped range from 2,926 meters at Beartooth Creek to 3,188 meters on Wyoming Creek. Two watersheds, Beartooth Creek and Canyon Creek, are on the west side of Beartooth Pass. The other two watersheds, Rock Creek and Line Creek, are on the east side (Figure 2). The distances between trapping locations are in the Appendix, Table 12. The confluence of Beartooth Creek and the Clarks Fork to the confluence of the Clarks Fork and Rock Creek outside of Rockvale, Montana is approximately 160 km. It is another 94 km from the confluence of the Clarks Fork and Rock Creek to the headwaters of Rock Creek (Appendix, Table 12).

Only Wyoming Creek, in the Rock Creek watershed, and Line Creek are grazed by livestock. The Line Creek allotment is grazed by 91 head of cow/calves from May 16

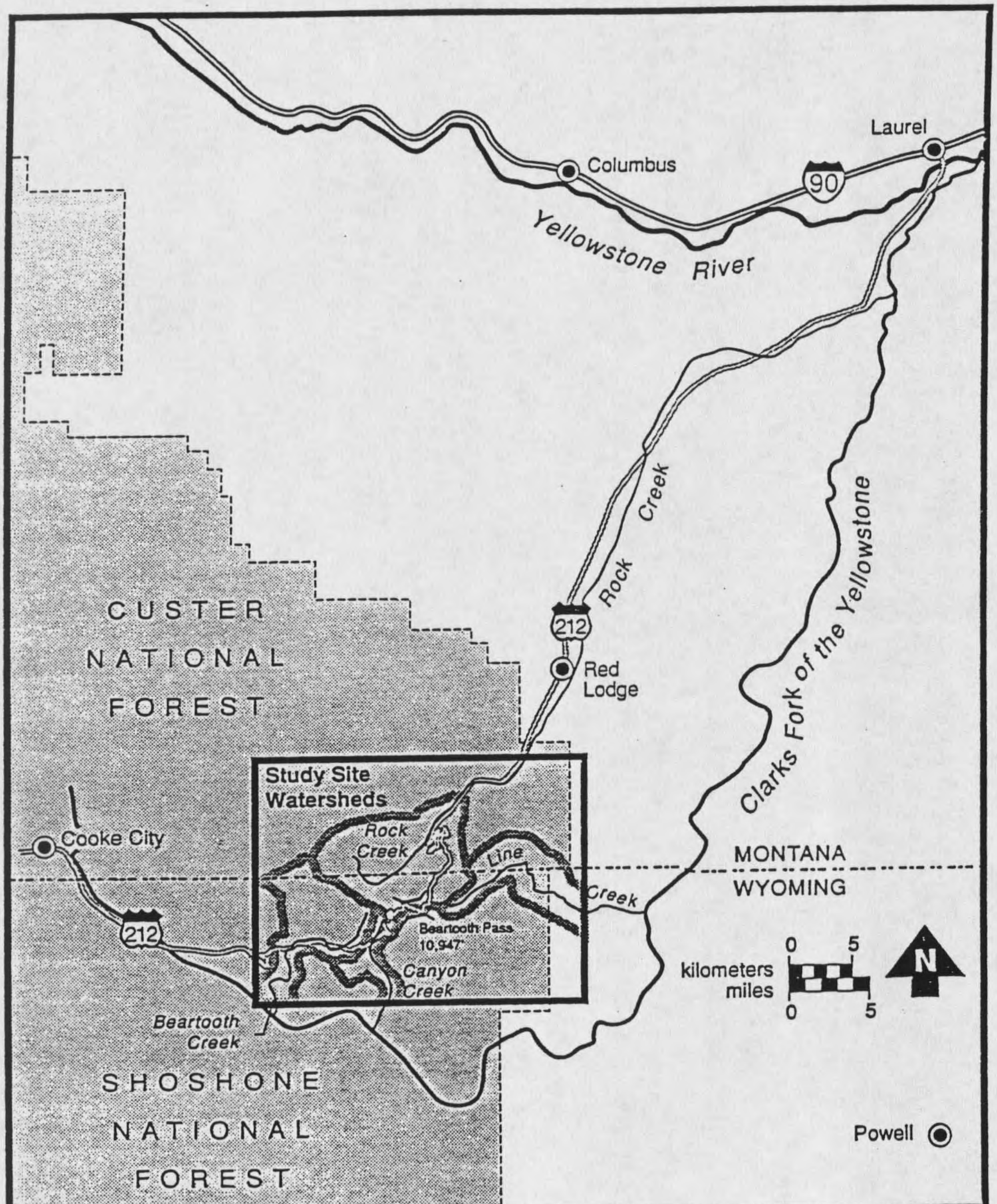

Figure 1. Regional map showing the headwaters of the Clarks Fork of the Yellowstone River.

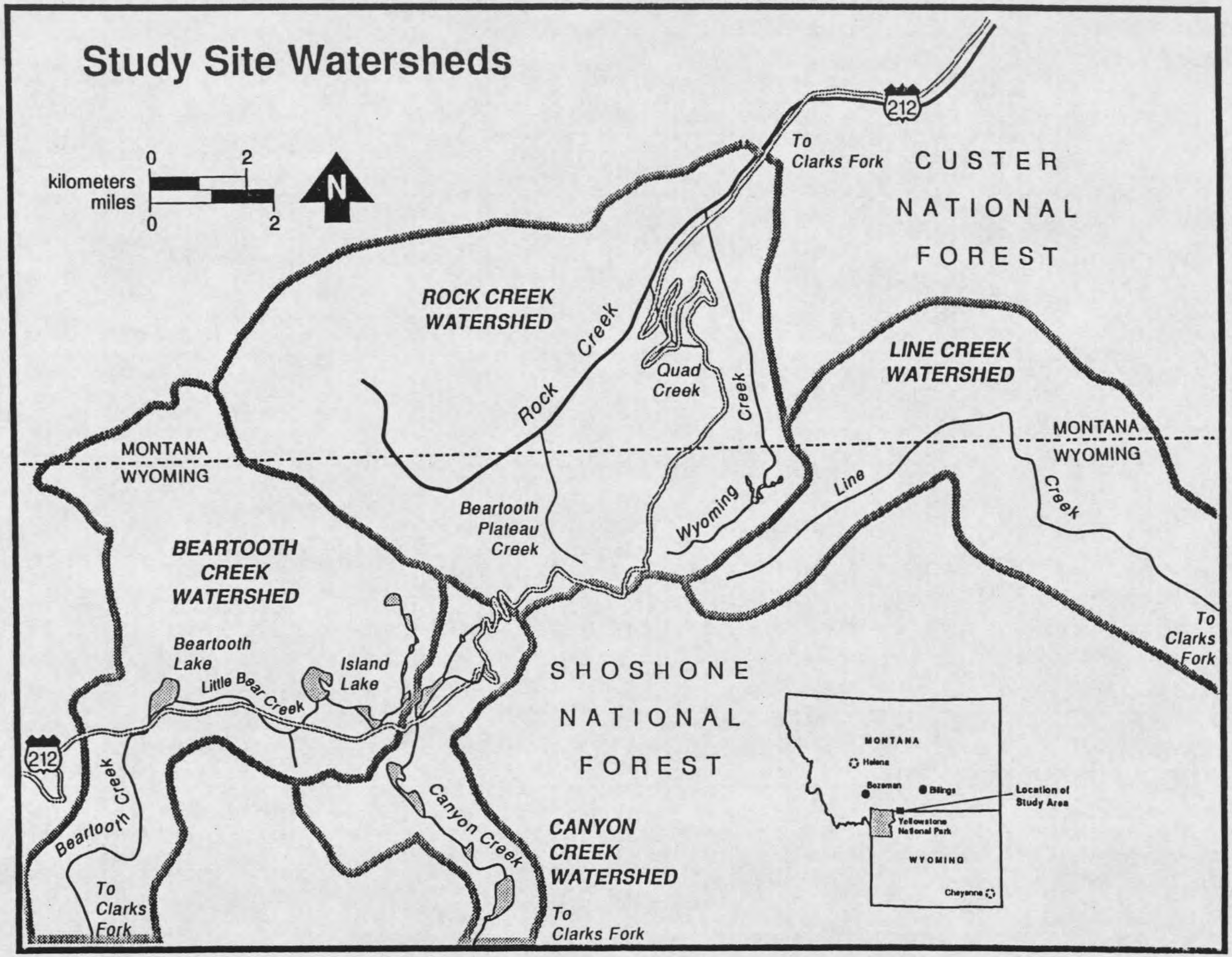

Figure 2. Area map of the study site watersheds.