Habitat selection and behavioral interactions of two sympatric voles Microtus montanus and Microtus pennsylvanicus

David Leon Genter

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HABITAT SELECTION AND BEHAVIORAL INTERACTIONS OF TWO SYMPATRIC VOLES, MICROTUS MONTANUS AND MICROTUS PENNSYLVANICUS.

by

David Leon Genter

B. A., cum laude, University of Colorado, 1982

Presented in partial fulfillment of the requirements for the degree of Master of Arts University of Montana 1986

Approved by

[Signatures]

Chairman, Board of Examiners

Dean, Graduate School

Date June 10, 1986

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Microhabitat Selection and Behavioral Interactions of Two Sympatric Voles, *Microtus montanus* and *Microtus pennsylvanicus* (49 pp.)

Director: Lee H. Metzgar

*Microtus pennsylvanicus* and *Microtus montanus* are sympatric throughout much of western Montana and adjacent states. This study investigated multiple sites throughout the range of sympathy to assess the interspecific ecological and behavioral influences on habitat selection of the two species.

*M. pennsylvanicus* was more mesophyllic in distribution than *M. montanus*. Both species were more eurytopic in allopatric populations. Range of habitats occupied was positively correlated with population density for each species. Geographic and temporal asynchrony in population cycles between species provided a dynamic continuum in habitat use patterns. Sites with low density populations for both species demonstrated habitat partitioning along a mesic-xeric gradient. Sites with high density of only one species exhibited an expansion in habitat use by that species, resulting in more extensive interspecific habitat overlap. Southern populations of *M. pennsylvanicus* were restricted to mesic sites while northern populations of *M. montanus* were rarely found occupying mesic sites.

Agonistic behavior was observed between and within species. Intra-sexually paired bouts were more aggressive than inter-sexually paired bouts. Population density was correlated with increased levels of aggression. Neither species was behaviorally superior in all situations.

Both intraspecific interactions and divergent habitat preferences appear to be important in maintaining separation between *M. pennsylvanicus* and *M. montanus* but the importance of each changes through population cycles. It is predicted that uniformly optimal habitats for one species will facilitate competitive exclusion of the other.
ACKNOWLEDGEMENTS

I thank the many individuals who have assisted me in this effort. John Higgins volunteered countless hours as a field assistant in 1983. Others contributing in field study, plant identification, or logistical support include Bryant Wood, Hugh Null, Bob Wood, Katie Duffy, Rick Jannett, Joan Bird, and chief compotator Pat Mullen.

The following individuals provided hospitable accommodations and allowed me access to their respective managed areas for study: Jon Malcolm, National Bison Range; Al Schulmeyer, Big Hole National Battlefield; Bob Wood, Grand Teton National Park; Doyle Markham, Idaho National Engineering Laboratory; and Ken Walker, Walker Ranch. Ken Diem provided use of the facilities at the University of Wyoming - National Park Service Research Center at Grand Teton National Park.

I would like to thank the members of the Zoology Department for providing the environment and space for my continuing education and growth. I am most grateful to my advisor, Lee Metzgar, for his help, tireless enthusiasm, and constructive criticism in guiding me through my graduate studies. I would like to thank the members of my committee Dick Hutto and Bart O'Gara for their contributions through these rites of passage. I particularly appreciate the support from everyone to pursue my extra-curricular research activities.
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INTRODUCTION

Various forms of niche separation between morphologically and ecologically similar species may serve to reduce interspecific competition. Within the framework of niche theory such differences relate to the principle of competitive exclusion that concerns the inability of ecological equivalents to coexist in a stable manner (Gause 1934). Grant (1972) noted that much of the evidence for interspecific competition in sympatric species falls into two categories: (a) two sympatric species exhibit an inverse numerical relationship, and (b) two sympatric species exhibit an inverse spatial relationship. A large number of studies demonstrate that ecologically similar, coexisting animal species differ in their habitat or microhabitat affinities (see review by Schoener 1974 for examples), and rodents are no exception (e.g. Rosenzweig and Winsburg 1969, Brown and Lieberman 1973, Kaufman and Fleharty 1974, M'Closkey and Fieldwick 1975, Rosenzweig et al. 1975, Douglass 1976, M'Closkey 1976, Dueser and Shugart, 1978, Price 1978, Holbrook 1979).

On theoretical and empirical grounds, habitat partitioning is considered the most common form of niche separation for sympatric species (MacArthur and Wilson 1967, Schoener 1974). Habitat differences are usually cited as being the primary factor allowing for multispecies coexistence (Schoener 1974, Cody 1978, Dueser and Shugart 1979).

Competition may be episodic or absent if severe climatolog-
ical or environmental events prevent species' numbers from approaching their resource-determined carrying capacity (Wiens 1977, Grant 1978, Rotenberry 1980) or if one population exhibits a widely fluctuating population density (Blaustein 1980). Should population fluctuations occur asynchronously over a wide geographic range, this could provide another mechanism where competing species might maintain a dynamic coexistence over a wide region of sympatry.

*Microtus montanus* (Peale) and *M. pennsylvanicus* (Ord) are morphologically similar rodents of the vole subfamily Microtinae. The meadow vole (*M. pennsylvanicus*) has the most extensive range of any North American species of the genus *Microtus* (Fig. 1), occurring throughout Canada, the northern and eastern United States, and as far south as Mexico (Hall 1981). It is most commonly found in grasslands, usually moist areas, but may also occur in woodland habitat. The montane vole (*M. montanus*) occurs widely in mountainous parts of the western United States (Fig 2). *M. montanus* typically inhabits moist meadows but is often found in grassy areas far from standing water (Rose and Birney 1985).

The geographic ranges of these two species overlap extensively in the northern Rocky Mountains (Anderson 1959), with several accounts of their coexistence in the same habitat (Findley 1951, Anderson 1954, Koplin and Hoffmann 1968, Douglass 1976). Their relative abundance and ease of capture make them ideal subjects for ecological field studies. Further-
Figure 1. Map of the distribution of *Microtus pennsylvanicus* (Modified from Hall 1981).
Figure 2. Map of the distribution of *Microtus montanus* (Modified from Hall 1981).
more, they possess a well defined repertoire of behavioral motor patterns which facilitate intra- and interspecific comparisons.

Competitive interactions between species of the genus Microtus have been documented (Cruzan 1968, Koplin and Hoffmann 1968, Murie 1971, Colvin 1970, Stoecker 1972, Conley 1976) and have produced conflicting results. Murie (1971) suggests M. pennsylvanicus is behaviorally dominant to M. montanus, thus restricting M. montanus to the drier sites (wet sites are 'preferred' habitat for M. pennsylvanicus). Stoecker (1972), however, indicates that M. montanus is dominant over M. pennsylvanicus and when M. montanus is removed from an area of potential contact, M. pennsylvanicus moves into more arid sites. This suggests that M. montanus excludes M. pennsylvanicus from arid sites. Koplin and Hoffmann (1968) used a removal technique but also provided a simultaneous control. Their results supported (nonstatistically) Murie's work. In summary, most authors suggest that behavioral dominance determines the spatial segregation of sympatric voles, with some studies concluding M. pennsylvanicus to be dominant to M. montanus (Cruzan 1968, Koplin and Hoffmann 1968, Murie 1971), while others find the reverse to be true (Colvin 1973, Stoecker 1972).

The conflicting literature on which species dominates may be due to geographic variability in the dominance relationship or to differences in the relative population levels during various
Figure 3. Map of sympatric distribution of *Microtus pennsylvanicus* and *M. montanus* with study site locations.
studies. Population density affects levels of intraspecific aggression in *Microtus* (Krebs 1970, Christian 1971) and may also affect interspecific aggression (Grant 1972, Conley 1976). Cyclic populations that undergo marked density fluctuations will experience varying levels of aggressive behavior. This, in turn, may cause different populations to exhibit various dominance scenarios. However, no study has yet related demographic and behavioral parameters to habitat use in sympatric microtine rodents.

Geographic differences in competitive abilities within species may be due to environmental, climatological, or genetic factors. Species at the edge of their range are presumably limited by one or more of these factors. In western Montana, both species are at the edge of their range of distribution. *M. pennsylvanicus* terminates its southern distribution in northwestern Wyoming while *M. montanus* reaches its northern limit near the National Bison Range in northwestern Montana (Fig. 3). The question of a geographic or regional effect in species interactions has been largely overlooked (Grant 1972) and rarely if ever tested. Furthermore, previous studies lack the uniformity needed to properly compare their results. Such a comparison would need contemporaneous study with comparable field methods. Here I examine the competitive relationships between *M. montanus* and *M. pennsylvanicus* at multiple sites simultaneously throughout their range of sympathy.

I investigated the behavioral interactions and habitat use
of *M. montanus* and *M. pennsylvanicus*, and I tested 2 hypotheses on competition between two species throughout their sympatric range. First, sympatric species will not partition their habitat identically across broad geographic areas. Second, population density influences the behavioral and competitive interactions between species. From these I predicted that:

1. habitat partitioning between the two species will vary regionally;
2. population fluctuations by either species will be accompanied by temporal variation in habitat use;
3. aggressive behavior will be directly proportional to population density; and
4. the species with the highest density will be behaviorally dominant over the other species.

**METHODS**

**Study sites**

My four study sites encompassed the latitudinal range of sympatric *M. pennsylvanicus* and *M. montanus*. Criteria for selection of sites were continuous grassland with minimum area of 7 ha, presence of a mosaic pattern of mesic and xeric conditions, relatively ungrazed, and the presence of one or both species.

Each site was mapped and a coordinate system was established for the location of individual stations. Stations were randomly selected from among grid points. Criteria for siting the trap stations were a minimum distance of 150 m between
stations (to minimize effects of removal on the resident population dynamics) and selecting microhabitat in proportion to its occurrence. Each station was numbered and permanently marked.

Three snaptraps, baited with peanut butter, were placed within 1 m of each station center. Traps were checked twice daily for 4 days. Captured voles were tagged, weighed, and frozen for later identification and examination. For each specimen I recorded species, sex, mass, age class (juv, ad), and adult reproductive condition (non-perforate, perforate, gravid, lactating, non-scrotal, scrotal, or other). Species were identified by means of the molar pattern (Hall and Kelson 1959, Lechlietner 1969).

Soil description

Each station was characterized with respect to moisture and vegetation. A series of 5 soil samples were taken from the upper 20 cm of the profile at each station using an Oakfield sampler. These samples were sealed individually and weighed before transport to the laboratory for analysis. I determined moisture content by a comparison of weights before and after drying the soil for 24 hr at 105 C. Soil moisture at each station, based on the average of the five individual samples, was determined by subtracting oven dry weight from the wet weight and dividing by the wet weight. I sampled all areas in July 1983, and August 1984, after a rainless period of at least
one week. Initially, I used the scaling method of Stoecker (1970), whereby a soil sample from each station was placed in one of five moisture categories, but found this method impractical.

Vegetation Description

I measured each station for canopy coverage and height and relative frequency of herbaceous species. I estimated canopy coverage and percent coverage of dominant plant species. Plant nomenclature follows Hitchcock and Cronquist (1973) and Weber (1972).

Numerous methods exist for the classification of plant communities, and the choice among classifications is largely arbitrary. I use three criteria for classification: species composition, physiognomy, and life form (Hanson and Churchill 1961). The classification of plant community types in this study is based on plant dominance (expressed as percentage of coverage and frequency of taxa) and to a lesser extent on soil moisture. The three most conspicuous plants in the herbaceous layer are defined as dominants for this classification.

Behavioral Description

Behavioral analyses were designed to measure aggressiveness. Voles were live-trapped at each site for subsequent paired encounters, where I observed behavioral responses between individuals. Sherman live-traps were placed in pairs between
snap-trap stations in active runways. Efforts were made to reduce or avoid the capture of individuals that may have had prior extensive contact. Therefore, live traps were placed at a minimum distance of 50 m. Also, after capture of a suitable contestant, the pair of traps was picked up, cleaned out and re-set at another location in the field. Each live-trap was baited with peanut butter and grasses. A mixture of cotton and polyurethane was provided for bedding material. Traps were checked twice daily.

Live-trapped voles were weighed, aged, sexed, and given identifying numbers. Each was housed separately in a wire mesh holding cage (25x12x10 cm) with moistened grass and kept in a cool site until use. Only adult voles (>25 grams) were used in the staged encounters. Obviously pregnant or lactating females were excluded. A maximum difference of 4 g body mass was permitted between contestants, and an effort to pair voles from different capture areas was maintained. Individuals were paired only once for either an intraspecific or interspecific encounter. All voles were run within 24 h of capture.

Individuals were selected for paired encounters on the basis of size and sex. Although species determination was not always known apriori, external morphological cues were used to attain a balance between numbers of intraspecific and interspecific encounters. All individuals were later sacrificed and identified to species by examination of molar patterns (Hall 1981).
A portable arena was set up in a sheltered area with short, dense grass cover. The arena consisted of a 60 cm high piece of 28 gauge galvanized sheet metal forming a circle 1 m in diameter. The inside wall was painted forest green.

Weather and temperature were recorded prior to each session. Light intensity and temperature played important roles in the activity level of the voles. Direct sunlight and low temperatures greatly reduced the mobility of individual voles. Therefore, individuals were run in indirect light conditions with temperatures ranging from 12 to 28°C.

Paired voles were introduced to the area and, after their initial encounter, allowed to interact freely for 7 min. Behavioral observations were recorded by 2 observers, 1 for each animal.

The classification of motor patterns and agonistic behavior components was developed through preliminary observations of paired encounters and by modification of a system used by Colvin (1973). Seven behavioral components were identified and described as follows:

1) Approach — animal moved its body in the direction of opponent with attention directed toward the opponent. This was typically initiated within 20 cm of the opponent.

2) Offense — body axis was held parallel to turf with head braced and facing toward opponent's head. This was initiated
within approximately 20 cm of the opponent from a stationary position and never involved physical contact.

3) Chase -- when one animal rapidly pursued a retreating animal.

4) Defense -- animal stood up on hind legs and often balanced on tail while holding forefeet off the ground. Animal may have leaned toward or away from opponent.

5) Attack -- a sudden and swift lunge toward an opponent from within approximately 20 cm of the opponent. Often accompanied by physical contact and biting but actual contact was not necessary.

6) Retreat -- rapid escape typically occurring after an attack, approach or threat from an opponent. This may be mutual or more commonly one animal alone is involved. This had to be initiated within approximately 30 cm of the opponent.

7) Wrestle -- both animals engaged in fighting. Typically the action was fast paced, with one or both animals rolling about. Biting occasionally occurred and usually was directed at the rump.

Contestants were individually scored by frequency of
occurrence for each behavioral component. The winner of each contest was determined immediately following the contest. Two primary criteria were used: First, the winning animal must have exhibited more locomotory activity than the losing animal. This activity was defined as moving about the enclosure freely, generally not associated with any of the above-listed behavioral components (i.e., retreat, chase). Second, the winner must also have scored a greater number of approach, offense, chase, and attack behaviors or postures than its opponent. In cases where there was doubt as to the winner, the contest was considered a draw.

Behavioral data were quantified by numbers of behavioral interactions of each category in the 7 min. bout. This allowed for a relative comparison of aggressiveness among populations. Also, it provided a means of measuring the intensity of aggression in intraspecific and interspecific encounters. Analyses were performed by comparing frequency of occurrence and outcome of bouts between individuals, sexes, and populations.

Field studies began in early June and continued through late September of each year. Each site was visited twice seasonally for 5-7 days per trip.

Statistical methods used in evaluation of data were taken from Sokal and Rohlf (1969). Nonparametric tests for comparing frequency distribution were chi-square and G-test. Computer analyses were performed using subprograms of SPSSX (SPSS Inc.)
1983) on the University of Montana's DEC computer.

**STUDY SITES**

The National Bison Range (NBR) is a 7504 ha National Wildlife Refuge in Lake and Sanders counties at the southern end of the Flathead Valley in northwestern Montana, approximately 80 km north of Missoula. The refuge is administered as a preserve for large ungulates, primarily the 500-600 bison (*Bison bison*). Bison, along with the other large herbivorous mammals, are managed to prevent overgrazing and range degradation through a rest-rotation grazing system.

The NBR approaches the northern limit of the range of sympatry between *M. pennsylvanicus* and *M. montanus*. This area varies in elevation from 789 to 1490 m. The area is a mixture of grasslands, upland forest, with small areas of well developed riparian habitat. Grasslands of the NBR have been characterized as palouse bunch grass prairie (Morris and Schwartz 1957). The plant ecology of the palouse prairie has been described by Mitchell (1957), while characteristics of the hydrosere vegetation in the Flathead Valley have been described by Lokemoen (1962).

After preliminary surveys and trapping, I selected an area north of Mission Creek for my study area. This area has rolling hills with sloughs draining to Mission Creek. It provided a mosaic of xeric and mesic conditions all along the
Figure 4. Map of the National Bison Range Study Site.
strip between Mission Creek and a service road along the northern fenceline (Fig. 4). Annual precipitation was 34.7 cm in 1983 and 26.0 cm in 1984, the 30 year average was 31.0 cm (U.S. Fish and Wildlife Service NBR Gauging Station).

The Big Hole National Battlefield (BHNB) is a 265.5 ha parkland, located in Beaverhead County, southwestern Montana, approximately 17 km west of Wisdom on Highway 43 in the Big Hole Valley. Elevation averages 1885 m. Grassland and willow bottom are the two major plant communities (Despain 1973). The grassland was described as an abandoned irrigated hay meadow, which was formerly a shrubby Cinquefoil-Idaho fescue shrubland, but this association was no longer present because the area was kept abnormally moist by seepage from irrigation ditches on the bench (Pierce 1982). Annual precipitation was 45.6 cm for 1983 and 49.4 cm for 1984 (National Park Service gauging station).

The graminoid community occupied 49 percent of the flood plain and the habitat type was *Deschampsia caespitosa / Carix spp.* (Pierce 1982), but the species composition was highly variable.

The bench had 2 primary communities, grassland and shrubland. The grassland comprised 60 percent of the bench and was *Festuca idahoensis / Agropyron spicatum* habitat type (Mueggler and Stewart 1980). The area was fenced and received low levels of grazing from deer (*Odocoileus hemionus*), elk (*Cervus elaphus*), and moose (*Alces alces*). For a more detailed description of the BHNB flora and physical features, see Pierce.
Figure 5. Map of the Big Hole National Battlefield Study Site.
The southernmost study area was in northwestern Wyoming, along the Snake River in Grand Teton National Park (GTNP). I used the former exhibition pasture also known as Buffalo Meadows, approximately 2 km southeast of Jackson Lake Junction. The elevation is 2060 m. GTNP approaches the southern boundary of the range of sympatry between M. pennsylvanicus and M. montanus (Fig. 3). Buffalo meadow is in the flood plain of the Snake River, cut through the alluvial outwash plain of the valley. The 12 ha site was predominantly flat with several small washout coulees intruding in from the River (Fig. 6). The north end abuted some willow thickets (Salix spp.). The wet northern end gradually gave way to the drier south end of the meadow. The dominant vegetation on the north end was Deschampsia cespitosa and Poa pratensis. The south, east, and west sides were dominated by Bromus intermedium, Poa pratensis, and Grassis alba. Carex nebraskensis and Carex spp. were found in the wettest areas. For further description of the flora of GTNP, see Shaw (1976).

The meadow received limited grazing from moose and pronghorn (Antilocapra americana). Annual precipitation for 1983 was 70.0 cm and 45.6 cm for 1984 (National Park Service gauging station at Moose, Wyoming).

The Bozeman study site was approximately 9 km north of Bozeman, in the Gallatin Valley at an elevation of 1625 m (Fig. 7). The soils are an outwash type from Tertiary
Figure 6. Map of the Grand Teton National Park Study Site.
sediments. Precipitation averages 45 cm annually (U.S. Weather Bureau Station 104402, Montana State University, Bozeman). I used an old field along Churn Creek which received light seasonal grazing from horses. Another site along the railroad tracks nearby was also used. Both sites had xeric and mesic conditions of nearly equal proportions. The two sites combined were approximately 13 ha.

The dominant vegetation was Poa pratensis and Bromus spp. with Carex nebraskensis and other sedges predominant in the wettest areas.

The Idaho National Engineering Laboratory (INEL) is located on the Upper Snake River Plain, approximately 130 km NW of Idaho Falls, Idaho. The INEL is a U.S. Department of Energy research facility and a National Environmental Research Park.

I selected a site adjacent to the manicured lawns of the Central Facilities Area (Fig. 8). The habitat was altered by intensive watering and fertilizing of the exotic grasses (Poa). M. montanus was at the peak of its population cycle in 1984 and provided an opportunity to observe the behavior of an allopatric population of this species at high density.

RESULTS

Field

During the 2 years of study 409 M. pennsylvanicus and 376 M. montanus were captured from the five study sites. Three of these sites, (NBR, BZMN, GTNP), had populations of both
Figure 7. Map of the Bozeman Study Site.
Figure 8. Map of the Idaho National Engineering Laboratory Study Site.
species. Allopatric populations of *M. pennsylvanicus* and *M. montanus* were at the BHNB and INEL, respectively. The number of each species captured at each site for both years is provided in Table 1.

Relative densities, measured as captures per trap-night, were determined for both years at all but the INEL population (Fig. 9). Relative density of *Microtus*, as measured by trap success, was significantly higher in 1983 than 1984 ($X^2 = 291$, $p < 0.005$). *Microtus* exhibited the sharpest decline in density at the NBR and BHNB.

Peak density of voles was asynchronous between sites. *Microtus* were most dense at the INEL site during July 1984 with a trap success rate equal to 68 per 100 trap nights. In the following text this success rate is presented as probability of capture (PC). All other populations reached peak density in July and/or August of 1983. The BHNB was next (PC = 0.57), followed by GTNP (PC = 0.36), the NBR (PC = 0.28, and BZMN (PC = 0.13) (see Fig. 9).

Sympatric populations exhibited extensive habitat overlap. Both species of *Microtus* were captured at the same station in 24.3 percent of the stations at the NBR, 36.5 percent at GTNP, and 34.7 percent at BZMN (see Table 2).

*M. montanus* also occupied a narrower soil moisture regime in 1984. No significant differences exist between years but a wider range of soil moisture associations was recorded for 1983 at all sites (Figs. 10 and 11).
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Table 1. Number of *Microtus pennsylvanicus* and *M. montanus* captured at each study site in 1983 and 1984. Relative density, expressed parenthetically as captures per trap night, is based on both samples for each year. M.p. = *Microtus pennsylvanicus*, M.m. = *Microtus montanus*.
Figure 9. Levels of population density at each site for 1983-84. Relative density expressed as captures per 100 trap nights. Each site represents both species pooled.
M. pennsylvanicus was found more frequently in wetter soils than M. montanus in areas of sympatry ($G = 10.76$, $p < 0.005$, Figs. 10 and 11). However, when the analysis includes the two allopatric populations, the distinction is less clear. For instance, the allopatric population of M. pennsylvanicus at the BHNB occupied a wider range of soil moistures than all the sympatric populations combined (Fig 10). M. pennsylvanicus occupied significantly dryer soils at the NBR than at BZMN or the BHNB ($G = 6.87$, $p < .05$). This relationship was observed in 1983 only. During 1984, a period of low density Microtus, M. pennsylvanicus occurred on wetter soils, on average, than the previous year ($G = 10.74$, $p < 0.01$). Comparison of data for both years within each site reveals that Microtus were more stenotopic at lower densities (see Figs. 10 and 11).

M. montanus, while occupying generally drier soils, exhibited a wider tolerance in soil moisture conditions. Between-site variability was high. M. montanus at the BZMN site occupied wet- to-dry soils but were more mesophyllic than the NBR population. M. montanus at the INEL site exhibited the widest range of soil moisture ranging 8 to 42 percent. Low values are characteristic of the arid sagebrush-grassland habitat; the higher values were from the periphery of manicured lawns where heavy irrigation occurred.

M. pennsylvanicus was also more stenotopic in sympatric populations. In 1983, M. pennsylvanicus occupied sites at the BHNB with soil moistures of 12 to 58 percent. All other sites
Figure 10. Soil moisture occupied by each species at each site in 1983. M.m. = M. montanus, M.p. = M. pennsylvanicus. Range of soil moistures represents minimum-maximum readings for each species at each site.
Figure 11. Soil moisture occupied by each species at each site in 1984. M.m. = M. montanus, M.p. = M. pennsylvanicus. Bold line represents 90% soil moisture readings.
combined ranged 24 to 56 percent soil moisture. However, in 1984, numbers and occupied range of *M. pennsylvanicus* declined. Many sites occupied in 1983 were devoid of voles in 1984. The breadth of soil moisture occupied also contracted, ranging 28 to 56 percent.

*M. pennsylvanicus* occupied areas with higher median cover than *M. montanus* (see Figs. 12 and 13). Continuous variables of measured vegetative cover placed in groups of three cover classes (0-50%, 55-75%, 80-100%) reveal that frequency of capture in these cover classes is significantly different between species at the NBR (*G* = 69.08, *p* < 0.001). While *M. pennsylvanicus* occurred in more dense cover than *M. montanus* at the other sites, none were significantly different.

Both allopatric populations occupied a wider range of vegetative cover than did any of the sympatric populations (Figs. 12 and 13). *M. montanus* was found to use areas with vegetative cover ranging 35 to 100 percent at the INEL (Fig 13). All other sites combined ranged 55 to 100 percent vegetative cover. *M. pennsylvanicus* was also found to occupy a wider range of vegetative cover in the absence of the other Microtus. Occupied vegetative cover ranged 55 to 100 percent at the BHN (Fig. 12).

**Behavioral**

Frequency of agonistic behavioral responses was significantly different among populations (*X^2 = 20.67, p*
Figure 12. Percent vegetative cover for each population in 1983. Range of vegetative cover represents minimum-maximum with 100% absolute maximum.
Figure 13. Percent vegetative cover for each population in 1984. Range of vegetative cover represents minimum-maximum.
The INEL site was the most aggressive population with more than twice as many agonistic acts per vole for each 7 minute bout as any other population (Table 2). The BHN B had about half as many, followed by the NBR, GTNP, and BZMN.

Overall, M. pennsylvanicus displayed more aggressive behavior than M. montanus ($X^2 = 12.91, p < 0.01$). Interspecifically paired bouts indicate that neither species dominated the other in all populations. M. pennsylvanicus was the dominant species at the NBR, winning 83 percent of the decided bouts (Table 3). Results from GTNP demonstrate that M. montanus was dominant over M. pennsylvanicus in 75 percent of the decided bouts. The population at BZMN displayed very little aggressive behavior and most bouts ended in a draw. M. pennsylvanicus did win the only decided interspecific bout.

Intra-sexually paired M. pennsylvanicus display more agonistic acts per bout than the same sex pairs ($X^2 = 88.60, p < 0.001$). Male vs. male bouts elicited the most aggressive behavior and physical contact. However, female-female aggression was not significantly different in frequency from male-male bouts ($X^2 = 0.85, p > 0.70$). Less physical contact was evident between females but agonistic postures and locomotory activities (offense, chase) were similar to those of males.

Agonistic acts by females directed toward males were more frequent than male toward female (Table 4). Females would typically display the defense and offense postures against
<table>
<thead>
<tr>
<th>POPULATION</th>
<th>RELATIVE DENSITY</th>
<th>RELATIVE AGGRESSION</th>
<th>INDEX OF OVERLAP</th>
<th>SPECIES RATIO (M.p.:M.m.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>BZMN</td>
<td>0.136</td>
<td>3.14</td>
<td>0.35</td>
<td>1.2:1</td>
</tr>
<tr>
<td>NBR</td>
<td>0.290</td>
<td>6.48</td>
<td>0.24</td>
<td>1.7:1</td>
</tr>
<tr>
<td>GTNP</td>
<td>0.348</td>
<td>5.78</td>
<td>0.37</td>
<td>1:4.7</td>
</tr>
<tr>
<td>BHNB</td>
<td>0.570</td>
<td>8.40</td>
<td>N/A</td>
<td>1:0</td>
</tr>
<tr>
<td>INEL</td>
<td>0.672</td>
<td>19.1</td>
<td>N/A</td>
<td>0:1</td>
</tr>
</tbody>
</table>

Table 2. Relative aggression, density, index of species overlap, and species ratio for each population at peak population levels. Relative density given as captures per trapnight; relative aggression given as the number of agonistic acts per 7 minute bout; index of overlap is the proportion of stations where both species were captured.
Figure 14. Aggressive behavior as a function of population density. Both species pooled for each site. Standard error represented by vertical lines.
Table 3. Interspecifically paired bouts between *M. montanus* and *M. pennsylvanicus* for each sympatric population. Numbers represent number of wins for each species or inconclusive result (draw) in bouts.
Table 4. Frequency of agonistic acts directed intra- and inter-sexually by *Microtus pennsylvanicus*. Numbers given as observed (OBS) and expected (EXP) frequency of agonistic behaviors from one vole to the other in each pairing. EXP = row total x column total/grand total. *** = $p < 0.005$. 

<table>
<thead>
<tr>
<th>CONTESTANTS</th>
<th>OBS</th>
<th>EXP</th>
<th>(OBS - EXP)²/EXP</th>
</tr>
</thead>
<tbody>
<tr>
<td>MALE &quot;&quot; MALE</td>
<td>53</td>
<td>29.68</td>
<td>18.32</td>
</tr>
<tr>
<td>MALE &quot;&quot; FEMALE</td>
<td>0</td>
<td>23.32</td>
<td>23.32</td>
</tr>
<tr>
<td>FEMALE &quot;&quot; FEMALE</td>
<td>44</td>
<td>20.68</td>
<td>26.30</td>
</tr>
<tr>
<td>FEMALE &quot;&quot; MALE</td>
<td>3</td>
<td>26.32</td>
<td>20.66</td>
</tr>
</tbody>
</table>

Chi Square = 88.60 ***
males. On only three occasions did either sex initiate fighting or inflict wounds on the other, two of these were females against males.

DISCUSSION

The asynchrony of population densities and the regional variability in habitat use suggest that the competitive interactions may be quite different in different populations.

The conflicting results between the Northern populations (Koplin and Hoffmann 1968, Murie 1971) and Southern populations (Stoecker 1970, 1972, Douglass 1976) of M. montanus and M. pennsylvanicus may be explained by interrelated demographic and geographic factors. The results from the National Bison Range (Koplin and Hoffmann 1968) did not adequately address the role of density of both species. M. montanus was at low density and M. pennsylvanicus was at high density during this period (Koplin 1962, Murie 1963). That M. pennsylvanicus was behaviorally dominant (Murie 1971) follows the predictions stated earlier. Stoecker (1970) found that a natural reduction in the number of M. montanus resulted in a shift in their distribution away from the wetter sites. Concurrently, the more numerous M. pennsylvanicus expanded their range into drier sites. This was interpreted as evidence of dominance by M. montanus over M. pennsylvanicus.

Elevated aggression and high number of one species allows it
to outcompete and dominate the other species. Asynchronous population cycles within and between species over their geographic range may account for observed differences in behavioral patterns. One species may be numerically and behaviorally dominant in one part of its range while at the same time be less numerous and behaviorally subordinate at a different place (or the same place at a different time). The conflicting results given above on dominance and competitive superiority simply may be regional variation in habitat partitioning due, in part, to asynchronous population densities.

*Microtus* densities peaked and declined over much of their range during the late summer and fall of 1983, and aggressive behavior of *Microtus* was positively correlated with density. There were two distinct high and low levels of aggressive behavior at each site corresponding with the peak (1983) and low (1984) densities, respectively. This is consistent with Krebs' (1970) work on the relationship of density regulation and behavioral changes in microtine populations.

At higher density populations, each species exhibited broader habitat use. As population density increased and voles approached carrying capacity, marginal habitats were occupied. In this study *M. pennsylvanicus* was more eurytopic in 1983 than in 1984. Similarly, *M. montanus* was found in both drier and wetter sites in 1983 than 1984.

Rose and Birney (1985) believe that vegetation, more than
any other environmental factor, determines the presence or absence and relative importance of *Microtus* in small mammal communities. Birney et al. (1976) discussed several attributes of vegetative cover for *Microtus*. They suggested that concealment from predators was of greatest importance. Optimum habitat of *M. pennsylvanicus* has been identified as areas where grasses comprise 50 percent or more of the vegetation and total canopy cover is at least 85 percent (Hodgson 1970). These areas were characterized by relatively high substrate moistures and well developed grassy-herbaceous canopy layers. *M. pennsylvanicus* in this study occurred most often in soils with 90-100 percent vegetative cover. Only those voles in the highest density populations were found to use other habitats.

*M. pennsylvanicus* occupies habitat with high vegetative cover and moist soils. Soil moisture may be of considerable importance, but how much of this is directly related to moisture or to vegetation has not been determined. Murie (1969) showed that *M. pennsylvanicus* preferred wet over dry substrates in the laboratory, but that *M. montanus* from the same area showed no preference.

The occupied habitat of *M. montanus* was not as readily delineated as that of *M. pennsylvanicus*. Characteristics of the habitat that correlated with the distribution of *M. pennsylvanicus* were poor predictors of the distribution of *M. montanus*. The greater range of habitat occupied by *M. montanus* suggests a wider ecological tolerance of this species. Findley
(1951, 1954) also found *M. montanus* to display this wider tolerance in Jackson Hole, Wyoming.

The distributional patterns of the two species showed considerable overlap in sympatric populations. These populations did not exhibit the well defined competitive segregation as reported by Koplin and Hoffmann (1968) or Findley (1951, 1954). That allopatric populations are more broad in their habitat use suggests that interspecific competition influences the habitat distribution of locally sympatric microtines. Other authors (Findley 1951, Cameron 1964) have reported that one species of microtine rodent may occupy habitats used by another in the absence of that species.

Similarly, interspecific competition between *M. pennsylvanicus* and *Clethrionomys gapperi* is thought to influence distributional patterns on islands in the St. Lawrence River and off the east coast of Canada. Some islands have *Microtus* and others have *Clethrionomys*. Cameron (1964) found that the species present lives in a wider range of habitats than would be found on the nearby mainland where the two species occur together. Cameron (1964) suggested that chance determined which species colonized which island, but that once established the resident species was able to prevent subsequent colonization by the other. Linzey (1984) found that *Synaptomys* expanded in number and range after natural and experimental declines of sympatric *Microtus*. Her conclusion was that microhabitat partitioning was due to active competition that
varied temporally in intensity.

Interspecific competition appeared to be responsible for differential habitat use between allopatric and sympatric populations in this study. Both allopatric populations occupied a significantly wider range of habitat and moisture gradients than any of the sympatric populations of either species. This habitat expansion may be due to the absence of the competing species, thus allowing an increase in niche breadth. This provides a strong argument for interspecific competition as the controlling factor in niche breadth and habitat use by species. Perhaps the best means of testing such a question is by experimental manipulation of populations. The current situation lends itself to manipulation; the allopatric populations occupy habitat apparently suitable for both species. If the other species were introduced to these sites, the habitat would presumably be partitioned along some mesic/xeric gradient. Also, the resident population would undergo habitat reduction and would eventually equilibrate at a level comparable to other sympatric populations.

Intraspecific competition may also determine the width of habitat range (Hilden 1965, Grant 1972). Low density populations occupy only optimal habitat. As populations increase, less favorable habitats are inhabited, in order of suitability. During 1983, populations were at peak densities in most areas. This coincides with the wider range of habitat occupied by both species. Conversely, when populations
declined the following year, the range of occupied habitats was reduced as well.

Field and laboratory studies on *Microtus* suggest that behavioral interactions may be important in maintaining microhabitat segregation. Although the results of the staged encounters do not clearly indicate that interactions between *M. pennsylvanicus* and *M. montanus* control their segregation into different microhabitats.

Intraspecific, intrasexual agonistic behavior is most intense and is doubtless a significant factor in maintaining spacing of residents of each sex. The elevated levels of aggressive behavior in high density populations may be for defense of territory or access to estrous females (Wolff 1985). It may also provide a competitive advantage for dispersing individuals. Aggressive individuals from expanding populations would more easily displace adjacent allospecific populations through numerical and behavioral dominance. In this cyclic expansion and contraction of habitat use, sympatric populations may demonstrate interspecific competition episodically.

Interspecific competition is not easily quantified (Grant 1972, Schoener 1983) and its relevance in temperate environments has been questioned (Wiens 1977, Rotenberry 1980). However, intraspecific competition via territoriality and aggression has been suggested as regulating population levels (Getz 1978, Madison 1980, Jannet 1981). Similarly, interspecific competition may determine the range of habitats
occupied and influence the species composition of communities.

The ability of M. montanus to occupy habitats only marginally acceptable to M. pennsylvanicus and to expand its habitat in the absence of M. pennsylvanicus suggests that M. montanus is a generalist compared with M. pennsylvanicus. Apparently, the fundamental niche of M. montanus includes that of M. pennsylvanicus in the Northern Rocky Mountains, but the realized niche in areas of sympatry is considerably narrower due to interference competition (Miller 1967, Grant 1972). This was demonstrated by M. montanus occupying mesic habitat in low and high densities, whereas M. pennsylvanicus occupied xeric habitat during high density periods only. This is further supported by the observation that when a generalist and specialist species engage in interference competition, the specialist usually prevents access to a resource (space) by the generalist (Colwell and Fuentes 1975).
LITERATURE CITED


Cameron, A.W. 1964. Competitive exclusion between the rodent genera *Microtus* and *Clethrionomys*. Evolution 18: 630-634.


