Spatial interactions and micro-habitat selections of two locally sympatric voles, Microtus montanus and Microtus pennsylvanicus

by Richard James Douglass

A thesis submitted to the Graduate Faculty in partial fulfillment of the requirements for the degree of DOCTOR OF PHILOSOPHY in Zoology
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Abstract:
Miorotus pennsylvanicus and M. montanus are sympatric in south central Montana, and in many habitats both species can be found living in apparently intermixed populations. This study was an attempt to assess the relative importance of interspecific interactions and habitat preferences in maintaining spatial separations between the two species.

Radioisotope telemetry experiments conducted in 20 X 20 m field enclosures showed the following. M. montanus demonstrated larger home ranges in the presence of M. pennsylvanicus than in single species treatments. Spacing between individuals was closer for M. montanus when alone as compared to mixed treatments. There was more overlap in M. montanus home ranges in single species treatments than in mixed treatments. M. montanus selected different vegetation when alone than in the presence of M. pennsylvanicus. The vegetation selected by each species was different from that selected by the other.

Enclosure experiments in which trapping methods were used indicated that there were no significant differences in emigration rates, survival rates, or weight changes for either species between single and mixed species treatments.

Trap lines outside of the enclosures indicated that the two species cohabited the area throughout the year and they had different habitat preferences.

Both interspecific interaction and divergent habitat preferences were found to be important in maintaining separations but the apparent importance of each changed along habitat gradients. As habitats become uniformly optimal for M. pennsylvanicust M. pennsylvanicus are able to exclude M. montanus from an area.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

Microtus pennsylvanicus and *M. montanus* are sympatric in south central Montana, and in many habitats both species can be found living in apparently intermixed populations. This study was an attempt to assess the relative importance of interspecific interactions and habitat preferences in maintaining spatial separations between the two species.

Radioisotope telemetry experiments conducted in 20 X 20 m field enclosures showed the following. *M. montanus* demonstrated larger home ranges in the presence of *M. pennsylvanicus* than in single species treatments. Spacing between individuals was closer for *M. montanus* when alone as compared to mixed treatments. There was more overlap in *M. montanus* home ranges in single species treatments than in mixed treatments. *M. montanus* selected different vegetation when alone than in the presence of *M. pennsylvanicus*. The vegetation selected by each species was different from that selected by the other.

Enclosure experiments in which trapping methods were used indicated that there were no significant differences in emigration rates, survival rates, or weight changes for either species between single and mixed species treatments.

Trap lines outside of the enclosures indicated that the two species cohabited the area throughout the year and they had different habitat preferences.

Both interspecific interaction and divergent habitat preferences were found to be important in maintaining separations but the apparent importance of each changed along habitat gradients. As habitats become uniformly optimal for *M. pennsylvanicus*, *M. pennsylvanicus* are able to exclude *M. montanus* from an area.

INTRODUCTION

Some of the most interesting biotic factors influencing small mammal communities are interactions among the different component species. Many investigators (Calhoun, 1963; DeLong, 1966; Lidicker, 1966; Morris, 1969; Heller, 1971; Grant, 1969, 1970, 1971 and others) have suggested that interspecific interactions occur among small mammals and that interactions can influence the distribution, population levels, and movements of the members of the community. The present study is an attempt to assess some of the effects of interspecific interaction on the movements and microhabitat selection of two species in a small mammal community.

Meadow voles *(Microtus pennsylvanicus)* and montane voles *(Microtus montanus)* are ideally suited for a study of interspecific interaction. These two species are broadly sympatric in the Rocky Mountain region of the United States and can be found coexisting in various habitats in south central Montana. Other factors making these species suitable for this type of study are their close phylogenetic affinity, habitat similarities, and the suggestions by other investigators that interactions may occur between these species (summarized by Koplin and Hoffman, 1968; and Hodgson, 1972).

Both Koplin and Hoffman (1968), in discussing competitive exclusion, and Hodgson (1972), in his discussion of habitat preferences, offered proximate factors that possibly are involved in maintaining species separations. These are habitat preferences (Hilden, 1965; Wecker, 1963; Harris, 1952), behavioral intolerance as a result of olfactory discrimination (Moore, 1965), interspecific competition (Findley, 1954; Getz, 1962), or some combination of these. Murie (1971) in a laboratory study found meadow voles to be dominant over montane voles and suggested that when they are sympatric this dominance relationship is important in maintaining habitat separations between the two species. Hodgson (1972), however, captured both species of voles in 31 of 59 plots and often in adjacent traps or in the same traps on separate nights. He suggested that meadow voles and montane voles were not demonstrating habitat segregation to the extent found in Wyoming by Findley (1951, 1954) or in western Montana by Koplin and Hoffman (1968). Hodgson (1972) felt that separation in relation to the mosaic of the habitat was of relative importance in maintaining the separations of the two species. He was unable, however, to determine the importance of social interaction in maintaining a separation in this mosaic.

In this study I attempted to infer the relative importance of both social interactions and habitat preferences in maintaining habitat separations between meadow voles and montane voles in an ecological situation where the habitat was suitable for both species. Large field enclosures were established in which movements and vegetation selection between single and double species treatments of radioactively tagged voles were used to estimate the relative importance of social interactions and habitat preferences. Further deductions were made by comparing inferred emigration rates, survival rates and weight changes of untagged voles in single and double species treatments.

METHODS

The study site is a shallow coulee in an alluvial bench in south central Montana, 10.4 km north of Bozeman. The area is a grassland intermixed with wild rose and Canadian thistle and is bordered on either side by wheat fields. I selected this area because montane voles and meadow voles both inhabit the area, and it has the space required to accomodate large field enclosures.

In the bottom of the coulee, four (20 X 20 m) field enclosures were constructed of 12.6 mm mesh hardware cloth extending 0.5 m into the ground and 0.5 m above the ground and capped with a vertical sheet of aluminum 35 cm high (Figures 1 and 2). The vegetation was mowed to within two centimeters of the soil surface in a strip one meter wide on both sides of the wire. Each enclosure was situated so that it contained parts of home ranges of both species of *Microtus* as determined by a preliminary trapping program. The enclosures were effective in preventing immigration and emigration of voles. Three voles were lost, presumably to predation, during the experiments. Only shrews were observed passing through the fence. All rodents residing within the enclosures were trapped out before any experiments were conducted.

Maxillary tooth features, as described by Hall and Kelson (1959), were used to distinguish between the two species of voles. Tooth features of live animals were examined by making tooth impressions in modeling clay. Every animal was examined by this method, and I

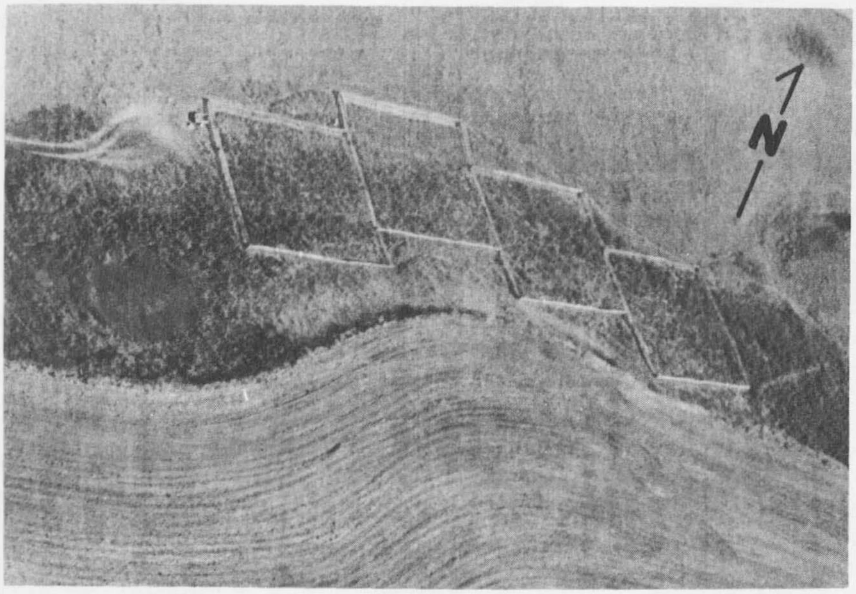

Figure 1. Aerial view of the four enclosures. Sides of the enclosures are 20 m long.

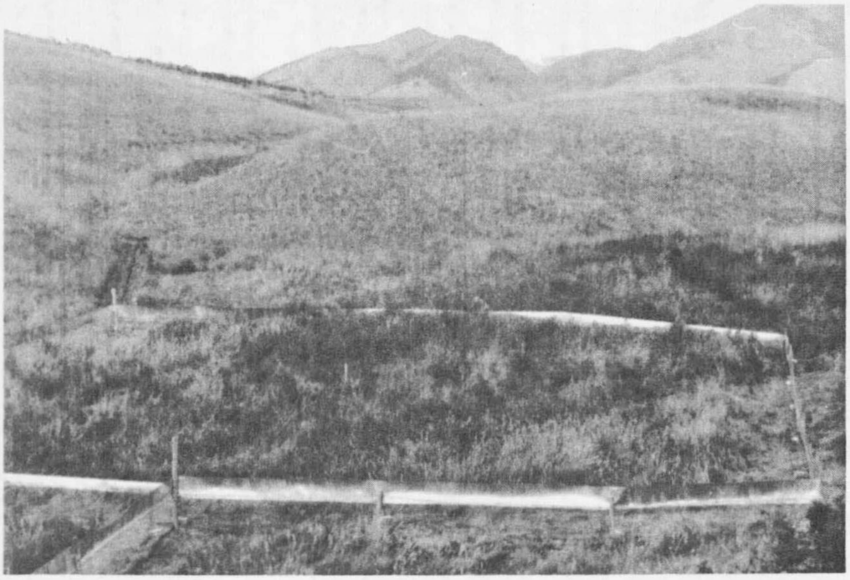

Figure 2. Ground view of enclosure 4. Height of fence is 85 cm.

avoided using animals that possessed intermediate dental characteristics. Only animals captured within three kilometers of the study area in habitats similar to the study area and containing both species of voles were used in this study. All statistical methods used in evaluation of data were taken from Woolf (1968).

Telemetry Experiments

The first series of experiments were conducted from July 20, 1971, to October 10, 1971, and again from February 16 to April 1, 1972. Radioactive tags were used to monitor the movements of the voles. To avoid complications caused by gravid females, only males were used in this series of experiments. The purpose of this series was to estimate the relative importance of habitat selection versus competitive exclusion by each species in single and mixed species groupings of voles. The following data were used for this estimate.

1. Home range size and overlap.
2. Distance among locations of all voles in an enclosure.
3. Vegetation near the points of location of voles of each species.

Animal movements within the enclosures were monitored by radioisotope telemetry as described by Godfrey (1953, 1954, 1955), Kaye (1961) and Harvey and Barbour (1965). A Ta^{182} wire, 2.5 to 10 mm in length and having an activity of 25, 50, or 100 μc, was implanted subcutaneously in each vole. The implantation technique was similar to that used on toads by Breckenridge and Tester (1961), and the safety precautions employed were the same as those used by Hirth, *et al.* (1969).

An Eberline model E-120 geiger counter with the scintillation probe attached to the end of a 2.4 m boom was used to locate the animals. The method of locating and discriminating among individuals was similar to that used by Ambrose (1967). Each animal was located at three separate times of day, each day, for the duration of the experiments. The location of an animal was marked by a flag placed 2.4 m from the animal and in line with a post located in the center of the enclosure. At the end of each of the tracking runs, the locations, approximate times, and weather conditions were recorded on maps of the enclosures.

Plant data were recorded for this series of experiments during August, 1971, by a method described by Daubenmire (1959). A two-by-ten decimeter frame was used to determine percentage canopy coverage and frequency of each plant species. The canopy coverage of each species was recorded as one of Daubenmire's six cover classes. Frames were placed at regular two meter intervals in a grid pattern with a total of 81 sampling sites per enclosure. The vegetation characteristics ascribed to a vole's location were those taken in the nearest plot of the 81 samples in each enclosure.

Each telemetry experiment was divided into two four-day tracking periods, A and B. Each enclosure was used for one of the following treatments: montane vole experimental, montane vole control, meadow vole experimental, and meadow vole control.

During Period A, the montane vole experimental enclosure contained two montane voles, one carrying a 25 μc tag, the other a 100 μc tag, and two meadow voles each carrying a 50 μc tag. In the meadow vole experimental enclosure two meadow voles carried either a 25 or 100 μc tag, and two montane voles carried 50 μc tags. Four montane voles were placed in the montane vole control enclosure, and four meadow voles were placed in the meadow vole control enclosure. Voles in the control enclosures were tagged in the same manner as those in the experimental enclosures. Of the four voles in each enclosure, I was able to distinguish among individuals tagged with 25, 50 and 100 μc tags but not between the two carrying 50 μc tags. The locations of animals carrying 50 μc tags were used for determining general vegetation description, home range overlap with the other two voles, and distances from the other two voles at the time they were located. For Period B the animals carrying 50 μc tags were exchanged between the two experimental enclosures, while the animals in the control enclosures were not moved. At the end of Period B a new experiment was started with all treatments being shifted to different enclosures. The experiment was repeated during the summer until each of the four treatments had been conducted in each of the four enclosures.

During the winter, four more experiments were conducted with only one modification from the summer experiments. I only tagged one of the four mice with a 100 μc wire in each enclosure because the snow made it impractical to distinguish among individuals. Montane voles were tagged in the montane vole experimental treatments and meadow voles were tagged in the meadow vole experimental treatments.

A total of 43 different voles were used in the summer series of experiments and 32 in the winter.

Emigration Experiments

The second series of experiments was conducted without the aid of radioactive tags from June 17 to September 2, 1972. To further assess the effect the two species had on each other the following data were collected from single and mixed species groupings.

1. Emigration rates (numbers of voles live-trapped along the enclosure fence).
2. Survival rates.
3. Weight changes.

The enclosures were slightly modified for these experiments. A one meter wide strip was rototilled along the inside periphery of each enclosure, and a two meter strip was mowed on the outside periphery of each. Bare ground similar to this three meter strip is rarely traversed by voles (Van Vleck, 1968, 1969), and I assumed that any voles venturing across the periphery were attempting to emigrate.

In order to capture animals attempting to emigrate, I set 24 live-traps in pairs back to back at intervals of 6.3 m along the inside of the fence of each enclosure. I washed the traps and then soaked them in strong detergent for three days before placing them in the enclosures to prohibit any residual smell of bait from luring the voles across the periphery. In attempting to avoid capturing animals that might incorporate the rototilled periphery in their normal nightly movements, the traps were opened only during the daylight hours.

Experiments were conducted at two densities, four voles per enclosure and eight voles per enclosure. Pairs of individually toe-clipped males and females that were not obviously gravid were used in all enclosures. In experiments with groups of four voles each of two experimental enclosures contained two pairs, one of each species. One control enclosure contained two pairs of montane voles, and the other contained two pairs of meadow voles. After four days the number of animals was doubled by adding voles in the same numbers and sex ratios as were initially placed in each respective enclosure. The second density was also maintained for four days. The live traps were opened for the last three days at each density of voles. Animals dying during any experiment were not replaced during that experiment. I recorded the number of each animal captured at the fence and then released it back into the enclosure. At the end of each experiment all animals were trapped and kept in cages in the coulee until the beginning of the next experiment. Animals were weighed at the beginning and end of each experiment. The experiments were repeated eight times with all enclosures having been used twice for each treatment. A total of 126 different individual voles were used during the course of these experiments.

Trap Lines

Trap lines covering a wider range of vegetational types than covered by the enclosures were set out in the coulee for the first five days of each month from April, 1972, to January, 1973. These trap lines served as natural controls for the enclosure experiments. The lines were intended to answer the following questions:

1. Were both the montane voles and meadow voles captured in close proximity to each other throughout the year?
2. What was the status of the populations of both species and what was their relative numbers?
3. Did habitat preferences exist between these two species over an area enclosed between both edges of the coulee?

Four parallel trap lines of 25 Sherman live traps each were set on contours approximately 100 m east of the enclosures. Trap line A was set along the north rim of the coulee, two lines, B and C, were set one-third and two-thirds of the way down the slope, respectively, and trap line D was set in the bottom of the coulee. Traps were checked three times daily at 0800, 1200, and 1800. The animals were toe-clipped and released. The species, sex, approximate age, location, time of capture and vegetation type were recorded for each animal. Four vegetation types were designated for the trap lines as follows: Type 1, sparse grass with gravelly soil readily visible; Type 2, sparse grass with fine grained soil readily visible; Type 3, dense grass, soil not visible, and litter layer less than 10 cm deep; and Type 4, dense grass, soil not visible, and litter layer deeper than 10 cm.

RESULTS

Telemetry Experiments

Home Range

Home ranges were measured on maps on which vole locations had been recorded. The boundaries of the home ranges were determined by a method similar to the minimum area method described by Mohr (1947) for trap-revealed home ranges. The areas enclosed by lines connecting locations were measured with the aid of a polar planimeter.

Table 1 shows the mean home range size in square meters for each species of vole. In both summer and winter the average home ranges of each species were larger in enclosures containing both species than in those containing a single species. However, the only statistically significant difference was found in the sizes of the summer home ranges of montane voles in experimental and control treatments.

I calculated the percentage of times voles carrying 50 μc tags were located within the summer home ranges of those carrying 100 and 25 μc tags (Table 2). The average frequency of overlap was higher in control treatments than experimental treatments for both species but statistically higher only in montane vole control treatments.

Spacing

The spatial arrangements among individual voles during the summer were estimated by determining the average distances separating locations

TABLE 1. AVERAGE HOME RANGE SIZES FOR MEADOW VOLES AND MONTANE VOLES DURING PERIOD A OF TELEMETRY EXPERIMENTS. Comparisons are made between control treatments of single species associations and experimental treatments having both species present.

	Control	Experimental	% of Control	N	t
		SUMMER			
Meadow vole	139.2[1]	164.0	117.8	14	0.57
Montane vole	76.5	171.7	224.4	16	9.40*
		WINTER			
Meadow vole	2.4	10.7	445.8	8	0.89
Montane vole	7.3	9.6	131.5	8	0.62

[1]Home ranges are expressed in square meters.

*P<0.01.

TABLE 2. OVERLAP IN SUMMER HOME RANGES DURING PERIOD A OF TELEMETRY EXPERIMENTS. Overlap was determined by calculating the percentage of times voles carrying 50 μc tags were located within the home ranges of those carrying 100 and 25 μc tags. Figures for experimental treatments represent percentage of overlap between home ranges of montane and meadow voles. Figures for control treatments are percentage of overlap between home ranges of voles of a single species.

Treatment	Experiments			
	Frequency of Overlap			
Meadow vole experimental	40.0	14.3	18.2	40.0
Meadow vole control	50.0	71.4	44.4	57.0
Montane vole experimental	42.4	0.0	22.3	6.2
Montane vole control*	68.2	33.3	50.8	40.6

*Indicates significantly more overlap in single species treatments than in double species treatments as determined by a 4 X 2 contingency table. $X^2 = 11.3$, df = 4, ($P<0.025$).

of voles recorded for each tracking period in a given enclosure. In the control treatments, measurements were taken from each vole carrying a 100 or 25 μc tag to the other two voles of the same species carrying 50 μc tags. In the experimental treatments, measurements were taken from the voles carrying 100 and 25 μc tags to the two voles of the other species carrying 50 μc tags. Table 3 shows that the intraspecific spacing was significantly closer than the interspecific spacing for both meadow voles and montane voles.

As an index of spacing home ranges, I determined the geometric centers of activity, a method similar to that of Hayne (1949), for each vole for both Periods A and B and measured the shifts in locations of the geometric centers from Period A to Period B. There were no significant shifts in centers of activity when the experimental enclosures were converted to single species enclosures (Table 4).

Vegetation Selection

A summary of data from 81 Daubenmire plots taken in each of the four enclosures is given in Table 12 in the Appendix. The numbers and kinds of species differ slightly among the enclosures, but the enclosures are similar with regard to the more common species. Four species of plants, *Agropyron repens*, *Poa pratensis*, *Artemisia ludoviciana* and *Rosa woodsii* occur most frequently in all four enclosures and also comprise most of the cover in each enclosure. An exception to this is *Cirsium arvense* which occurs frequently in enclosures three and four

TABLE 3. AVERAGE SPACING OF VOLES DURING PERIOD A OF TELEMETRY EXPERIMENTS IN THE SUMMER. Spacing is expressed as the average distance from voles carrying 100 and 25 μc tags to those carrying 50 μc tags that were located during the same tracking run. Control values represent intraspecific spacing and experimental values represent interspecific spacing.

	Control	Experimental	Difference	N	t
Meadow vole	6.25 m	9.6 m	53.6%	8	3.50*
Montane vole	6.24 m	8.0 m	28.0%	16	2.99*

*P<0.05

TABLE 4. AVERAGE SHIFTS IN GEOMETRIC CENTERS OF ACTIVITY BETWEEN PERIOD A AND PERIOD B OF TELEMETRY EXPERIMENTS.

	Control	Experimental	N	t
		SUMMER		
Meadow vole	2.5 m	4.7 m	10	1.13
Montane vole	3.3 m	3.5 m	16	0.17
		WINTER		
Meadow vole	1.1 m	1.1 m	3	0.00
Montane vole	7.8 m	2.4 m	3	1.08

but is not present in enclosures one and two.

Vegetation selection by voles was estimated by comparing the vegetation in plots nearest the recorded locations of voles in a given enclosure to all 81 plots taken during the general vegetation sampling for that enclosure. In doing this I am assuming that the vegetation in plots nearest the locations of voles was representative of the vegetation selected by the voles and that the vegetation found in the 81 plots taken in grid fashion was representative of the vegetation of the enclosure. Table 5 compares the overall frequencies of vegetation from each enclosure with the frequencies of vegetation selected by voles of both species and in both treatments. The sums of chi-square values for meadow vole control and experimental treatments were 78.83, df = 45, ($P<0.005$), and 59.86, df = 45, ($P<0.10$), respectively. Corresponding values for montane vole control and experimental treatments were 125.30, df = 45, ($P<0.005$) and 300.55, df = 46, ($P<0.005$), respectively. Meadow voles showed selection in two of the four enclosures and in one of the four enclosures in control and experimental treatments, respectively. Montane voles were selective in two of the four enclosures and in three of the four enclosures in control and experimental treatments, respectively. Both species demonstrated selection, but meadow voles were not selective in experimental treatments. The observed pattern of vegetation selected by both species of voles was not highly consistent among the enclosures. No single species of plant was selected