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
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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.

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RICHARD JAMES DOUGLASS

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Approved:

Head, Major Department

Chairman, Examining Committee

Graduate Dean

MONTANA STATE UNIVERSITY
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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 μ c, 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 μ c tag, the other a 100 μ c tag, and two meadow voles each carrying a 50 μ c tag. In the meadow vole experimental enclosure two meadow voles carried either a 25 or 100 μ c tag, and two montane voles carried 50 μ c 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 μ c tags but not between the two carrying 50 μ c tags. The locations of animals carrying 50 μ c 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 μ c 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 μ c 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 μ c tags were located within the summer home ranges of those carrying 100 and 25 μ c 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

¹Home 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 μ c tags were located within the home ranges of those carrying 100 and 25 μ c 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. $\chi^2 = 11.3$, $df = 4$, ($P < 0.025$).

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 μ c tag to the other two voles of the same species carrying 50 μ c tags. In the experimental treatments, measurements were taken from the voles carrying 100 and 25 μ c tags to the two voles of the other species carrying 50 μ c 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 μ c tags to those carrying 50 μ c 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

TABLE 5. COMPARISONS OF FREQUENCIES OF PLANT SPECIES FOUND NEAR VOLE LOCATIONS WITH THE GENERAL VEGETATION OF EACH ENCLOSURE. Comparisons are made with the number of plots in which a given species of plant was found.

	MEADOW VOLE CONTROL TREATMENT												MONTANE VOLE CONTROL TREATMENT											
	Enclosure 1			Enclosure 2			Enclosure 3			Enclosure 4			Enclosure 1			Enclosure 2			Enclosure 3			Enclosure 4		
	Encl. ¹	Vole ²		Encl.	Vole		Encl.	Vole		Encl.	Vole		Encl.	Vole		Encl.	Vole		Encl.	Vole		Encl.	Vole	
	Plots (N=81)	Plots (N=24)	X ²	Plots (N=81)	Plots (N=27)	X ²	Plots (N=81)	Plots (N=16)	X ²	Plots (N=81)	Plots (N=12)	X ²	Plots (N=81)	Plots (N=10)	X ²	Plots (N=81)	Plots (N=31)	X ²	Plots (N=81)	Plots (N=16)	X ²	Plots (N=81)	Plots (N=30)	X ²
<i>Agropyron repens</i>	20	5	0.14	35	12	0.01	52	14	0.56	43	7	0.05	20	1	0.90	35	1	11.67	52	14	1.35	43	6	6.35
<i>Phleum pratense</i>	2	4	19.71	7	6	5.60	22	4	0.71	19	3	0.01	2	0	0.24	7	11	25.50	22	4	0.03	19	8	0.11
<i>Poa pratensis</i>	81	24	0.00	79	27	0.00	81	16	0.00	80	12	0.00	81	10	0.00	79	31	0.00	81	16	0.00	80	30	---
<i>Achillea millefolium</i>	0	0	---	2	0	0.77	1	0	0.31	0	0	---	0	0	---	2	0	0.78	1	0	0.20	0	0	---
<i>Artemisia ludoviciana</i>	33	6	1.47	35	9	0.66	19	3	1.42	31	4	0.09	33	1	2.34	35	6	4.25	19	3	0.15	31	5	2.50
<i>Balsamorhiza sagittata</i>	1	0	0.29	0	0	---	0	0	---	0	0	---	1	0	0.10	0	0	---	0	0	---	1	0	0.37
<i>Cirsium arvense</i>	0	0	---	0	0	---	25	2	0.69	18	4	0.63	0	0	---	0	0	---	25	2	1.74	18	19	22.58
<i>Erigeron divergens</i>	14	1	2.34	28	1	7.90	14	5	1.66	17	0	2.55	14	1	0.29	28	1	8.89	14	5	1.81	17	2	3.02
<i>Lactuca serriola</i>	0	0	---	0	0	---	3	0	0.92	2	0	0.30	0	0	---	0	0	---	3	0	0.59	2	0	0.75
<i>Gaura coccinea</i>	0	0	---	1	0	0.39	0	0	---	0	0	---	0	0	---	1	0	0.39	0	0	---	0	0	---
<i>Geranium viscosissimum</i>	18	7	0.55	16	5	0.03	10	0	3.10	8	0	1.20	18	2	0.07	16	5	0.23	10	0	1.97	8	0	3.00
<i>Solidago missouriensis</i>	8	0	2.36	11	1	1.97	9	0	2.78	1	0	0.15	8	0	0.98	11	0	4.26	9	0	1.78	1	0	0.37
<i>Thlaspi arvense</i>	0	0	---	0	0	---	1	0	0.31	1	0	0.15	0	0	---	0	0	---	1	0	0.20	1	0	0.37
<i>Tragopogon dubius</i>	0	0	---	2	0	0.78	5	1	1.50	1	0	0.15	0	0	---	2	0	0.39	5	1	0.01	1	0	0.37
<i>Rosa woodsii</i>	56	23	2.48	34	23	11.59	40	8	0.22	43	5	0.33	56	9	0.64	34	24	8.84	40	8	0.01	43	25	4.91
Total			29.34*			29.70*			14.18			5.61			5.56			65.20*			9.84			44.70*
	MEADOW VOLE EXPERIMENTAL TREATMENT												MONTANE VOLE EXPERIMENTAL TREATMENT											
	Enclosure 1			Enclosure 2			Enclosure 3			Enclosure 4			Enclosure 1			Enclosure 2			Enclosure 3			Enclosure 4		
	Encl. ¹	Vole ²		Encl.	Vole		Encl.	Vole		Encl.	Vole		Encl.	Vole		Encl.	Vole		Encl.	Vole		Encl.	Vole	
	Plots (N=81)	Plots (N=30)	X ²	Plots (N=81)	Plots (N=28)	X ²	Plots (N=81)	Plots (N=31)	X ²	Plots (N=81)	Plots (N=28)	X ²	Plots (N=81)	Plots (N=42)	X ²	Plots (N=81)	Plots (N=34)	X ²	Plots (N=81)	Plots (N=29)	X ²	Plots (N=81)	Plots (N=31)	X ²
<i>Agropyron repens</i>	20	6	0.26	35	7	2.14	52	22	0.22	43	16	0.06	20	0	10.36	35	9	2.04	52	26	2.86	43	12	1.28
<i>Phleum pratense</i>	2	2	2.14	7	2	0.06	22	8	0.02	19	5	0.41	2	0	1.03	7	12	28.55	22	5	1.06	19	14	5.88
<i>Poa pratensis</i>	81	30	0.00	79	28	0.00	81	31	0.00	80	28	0.00	81	42	0.00	79	33	0.00	81	29	0.00	80	31	0.00
<i>Achillea millefolium</i>	0	0	---	2	0	0.69	1	0	0.40	0	0	---	0	0	---	2	0	0.82	1	0	0.36	0	0	---
<i>Artemisia ludoviciana</i>	33	11	0.12	35	15	0.70	19	4	1.46	31	15	1.59	33	3	13.34	35	6	4.92	19	2	3.39	31	7	2.08
<i>Balsamorhiza sagittata</i>	1	0	0.37	0	0	---	0	0	---	0	0	---	1	0	0.52	0	0	---	0	0	---	1	0	0.39
<i>Cirsium arvense</i>	0	0	---	0	0	---	25	12	0.60	18	6	0.01	0	0	---	0	0	---	25	12	1.08	18	10	1.37
<i>Erigeron divergens</i>	14	2	1.97	28	6	1.39	14	0	5.40	17	5	0.15	14	1	5.39	28	7	1.79	14	0	5.00	17	5	0.39
<i>Lactuca serriola</i>	0	0	---	0	0	---	3	0	1.10	2	0	0.70	0	0	---	0	0	---	3	6	31.65	2	2	2.02
<i>Gaura coccinea</i>	0	0	---	1	0	0.34	0	0	---	0	0	---	0	0	---	1	2	6.20	0	0	---	0	0	---
<i>Geranium viscosissimum</i>	18	4	1.02	16	3	1.16	10	1	2.06	8	2	0.23	18	0	9.33	16	2	2.93	10	0	3.60	8	1	1.42
<i>Solidago missouriensis</i>	8	0	2.96	11	1	2.06	9	0	3.40	1	0	0.35	8	0	4.15	11	4	0.05	9	2	0.46	1	0	0.39
<i>Thlaspi arvense</i>	0	0	---	0	0	---	1	0	0.40	1	0	0.35	0	0	---	0	0	---	1	0	0.36	1	0	0.39
<i>Tragopogon dubius</i>	0	0	---	2	0	0.69	5	6	8.84	1	0	0.35	0	0	---	2	0	0.82	5	17	129.00	1	0	0.39
<i>Rosa woodsii</i>	56	24	0.53	34	23	10.77	40	18	0.48	43	20	1.63	56	42	5.83	34	23	5.68	40	10	1.29	43	20	0.69
Total			9.37			20.00			24.38*			5.83			49.95*			53.80*			180.11*			16.69

*Connotes a significance level of less than 0.05.

¹Represents the number of plots in which a given species of plant was found of 81 plots taken at regular intervals.²Represents the number of plots in which a given species of plant was found nearest vole locations.

for or against consistently in all enclosures. Of the 15 plant species listed in the enclosures, ten were in plots located nearest the recorded locations of meadow voles. The average number of plant species in those plots was 7.5 per enclosure. Comparable figures for montane voles were 12 species of plants and an average of 7.3 per enclosure.

Table 6 shows the comparisons of vegetation selected by voles between experimental and control treatments. The chi-square values of all enclosures were added together for each species of vole. Meadow voles showed significant differences within only one of the four enclosures. The summed chi-square value for all enclosures of 34.27, $df = 34$, ($P < 0.25$) indicates that, for the four enclosures, the vegetation selected by meadow voles during experimental treatments was not significantly different from that selected during control treatments. Montane voles showed significant differences within three of the four enclosures, and the summed chi-square value for all enclosures of 68.47, $df = 34$, ($P < 0.005$) indicates that they demonstrated significantly different selections during experimental treatments than during control treatments. The vegetation selected by montane voles was not consistent from enclosure to enclosure, but there was an average of 10% more species found in plots near locations of montane voles in experimental treatments than in control treatments. There were no differences between control and experimental treatments in the average number

TABLE 6. COMPARISON OF FREQUENCIES OF PLANT SPECIES FOUND IN PLOTS NEAREST VOLE LOCATIONS IN EXPERIMENTAL TREATMENTS WITH PLOTS NEAREST VOLE LOCATIONS IN CONTROL TREATMENTS WITHIN EACH ENCLOSURE.

	Enclosure 1			Enclosure 2			Enclosure 3			Enclosure 4		
	Cont. ¹	Exp. ²	X ²	Cont.	Exp.	X ²	Cont.	Exp.	X ²	Cont.	Exp.	X ²
MEADOW VOLE CONTROL VS. EXPERIMENTAL												
Plots ³	32	30		27	28		25	31		12	28	
<i>Agropyron repens</i>	9	6	0.36	12	7	1.75	13	22	0.87	7	16	0.01
<i>Phleum pratense</i>	7	2	2.40	6	2	2.33	9	8	0.43	3	5	0.23
<i>Poa pratensis</i>	32	30	0.00	27	28	0.00	25	31	0.00	12	28	0.00
<i>Achillea millefolium</i>	--	--	--	--	--	--	--	--	--	--	--	--
<i>Artemisia ludoviciana</i>	10	11	0.37	9	15	1.06	3	4	0.02	4	15	0.73
<i>Balsamorhiza sagittata</i>	--	--	--	--	--	--	--	--	--	0	2	0.60
<i>Cirsium arvense</i>	--	--	--	--	--	--	10	12	0.01	4	6	0.47
<i>Erigeron divergens</i>	1	2	0.42	1	6	3.19	7	0	8.56	0	5	2.14
<i>Lactuca serriola</i>	--	--	--	--	--	--	--	--	--	--	--	--
<i>Gaura coccinea</i>	--	--	--	--	--	--	--	--	--	--	--	--
<i>Geranium viscosissimum</i>	10	4	2.12	5	3	0.67	0	1	0.82	1	2	0.02
<i>Solidago missouriensis</i>	--	--	--	1	1	1.83	1	0	0.82	--	--	--
<i>Thlaspi arvense</i>	--	--	--	--	--	--	--	--	--	--	--	--
<i>Tragopogon dubius</i>	--	--	--	--	--	--	3	6	0.49	--	--	--
<i>Rosa woodsii</i>	30	24	0.28	23	23	0.08	14	8	0.02	5	20	1.19
Total			5.95			10.91			12.03*			5.38
MONTANE VOLE CONTROL VS. EXPERIMENTAL												
Plots	10	42		31	33		16	29		30	31	
<i>Agropyron repens</i>	1	0	4.26	1	9	5.78	14	26	0.02	6	12	1.87
<i>Phleum pratense</i>	--	--	--	11	12	0.01	4	5	1.06	8	14	1.41
<i>Poa pratensis</i>	10	42	0.00	31	33	0.00	16	29	0.00	30	31	0.00
<i>Achillea millefolium</i>	--	--	--	--	--	--	--	--	--	--	--	--
<i>Artemisia ludoviciana</i>	1	3	0.10	6	6	0.02	3	2	1.25	5	7	0.37
<i>Balsamorhiza sagittata</i>	--	--	--	--	--	--	--	--	--	--	--	--

TABLE 6. (Continued).

	Enclosure 1			Enclosure 2			Enclosure 3			Enclosure 4		
	Cont.	Exp.	X ²	Cont.	Exp.	X ²	Cont.	Exp.	X ²	Cont.	Exp.	X ²
<i>Cirsium arvense</i>	--	--	----	--	--	----	2	12	2.86	19	20	3.16
<i>Erigeron divergens</i>	1	1	1.25	1	7	4.04	5	0	8.89	2	5	1.17
<i>Lactuca serriola</i>	--	--	----	--	--	----	0	6	3.37	0	2	1.92
<i>Gaura coccinea</i>	--	--	----	--	--	----	--	--	----	--	--	----
<i>Geranium viscosissimum</i>	2	0	8.53	5	2	1.54	--	--	----	0	1	0.96
<i>Solidago missouriensis</i>	--	--	----	0	4	2.69	0	2	1.32	--	--	----
<i>Thlaspi arvense</i>	--	--	----	0	2	1.85	--	--	----	--	--	----
<i>Tragopogon dubius</i>	--	--	----	--	--	----	1	17	7.24	--	--	----
<i>Rosa woodsii</i>	9	42	0.06	24	23	0.17	8	10	0.56	25	20	0.77
Total			14.20*			16.07*			26.57*			11.63

¹Control treatment with one species of vole present in the enclosure.

²Experimental treatment with both species of voles present in the enclosure.

³Number of plots nearest locations of voles.

*Connotes a significance level of $P < 0.05$.

of plant species in plots near meadow vole locations.

A comparison of vegetation in each enclosure selected by meadow voles with that selected by montane voles during experimental treatments is shown in Table 7. The chi-square values of three of the enclosures and the sum chi-square values of all enclosures (74.72, $df = 36$, $P < 0.005$) indicate that the vegetation selected by these two species of voles differed significantly.

Emigration Experiments

Emigration Tendencies

Emigration was inferred by two methods, the average number of captures at the periphery of the enclosures, and the number of different individual animals captured at the periphery. Table 8 shows the average number of captures per experiment for both species, both experimental and control treatments, and both densities. Emigration rates in experimental treatments were not significantly different from those in control treatments for either species of voles at either density. I pooled the number of meadow voles and montane voles at the density of four per enclosure and compared the combined captures with the combined captures at eight per enclosure. Table 8 shows a higher capture rate at the higher density, but the difference in the rates is not statistically significant.

Table 9 shows the total number of different individual voles that were captured at the periphery during the experiments. The results of

TABLE 7. COMPARISON OF FREQUENCIES OF PLANT SPECIES SELECTED BY MONTANE VOLES WITH THAT SELECTED BY MEADOW VOLES WITHIN EACH ENCLOSURE. Comparisons are made of the plant species found in plots nearest the locations of each species of vole under experimental treatments.

	Enclosure 1			Enclosure 2			Enclosure 3			Enclosure 4		
	Mont- ane	Mead- ow	X ²	Mont- ane	Mead- ow	X ²	Mont- ane	Mead- ow	X ²	Mont- ane	Mead- ow	X ²
Plots ¹	42	30		33	28		29	31		31	28	
<i>Agropyron repens</i>	0	6	8.40	9	7	0.04	26	22	0.75	12	16	1.11
<i>Phleum pratense</i>	0	2	2.20	12	2	5.56	5	8	0.44	14	5	3.40
<i>Poa pratensis</i>	42	30	0.00	33	28	0.00	29	31	0.00	31	28	0.00
<i>Achillea millefolium</i>	--	--	--	--	--	--	--	--	--	--	--	--
<i>Artemisia ludoviciana</i>	3	11	7.60	6	15	4.90	2	4	0.54	7	15	4.99
<i>Balsamorhiza sagittata</i>	--	--	--	--	--	--	--	--	--	0	2	1.77
<i>Cirsium arvense</i>	--	--	--	--	--	--	12	12	0.04	10	6	0.38
<i>Erigeron divergens</i>	1	2	0.37	7	6	0.00	--	--	--	5	5	0.03
<i>Lactuca serriola</i>	--	--	--	--	--	--	6	0	6.40	2	0	1.77
<i>Gaura coccinea</i>	--	--	--	--	--	--	--	--	--	--	--	--
<i>Geranium viscosissimum</i>	0	4	5.40	2	3	2.01	0	1	0.92	1	2	0.54
<i>Solidago missouriensis</i>	--	--	--	4	1	1.72	2	0	2.17	--	--	--
<i>Thlaspi arvense</i>	--	--	--	2	0	1.70	--	--	--	--	--	--
<i>Tragopogon dubius</i>	--	--	--	--	--	--	17	6	6.27	--	--	--
<i>Rosa woodsii</i>	42	24	0.97	23	23	0.28	10	18	1.99	20	20	0.06
Total			24.94*			16.21*			19.52*			14.05

¹Plots found nearest locations of voles.

*Connotes a significance level of P<0.05.

TABLE 8. AVERAGE NUMBER OF CAPTURES OF VOLEs AT THE EDGES OF THE ENCLOSURES DURING THE EMIGRATION EXPERIMENTS. Captures from all enclosures are averaged together for both control and experimental treatments.

	Control	Experimental	N	t
4 VOLEs PER ENCLOSURE				
Meadow vole	2.6	2.2	8	0.21
Montane vole	2.1	3.4	8	0.80
t	0.29	0.63		
8 VOLEs PER ENCLOSURE				
Meadow vole	3.9	5.8	8	0.87
Montane vole	4.0	5.5	8	0.51
t	1.41	1.21		
4 VOLEs VERSUS 8 VOLEs PER ENCLOSURE ¹				
4 voles/ enclosure	4.7	5.6	8	
8 voles/ enclosure	7.9	8.9	8	
t	1.39	1.20		

¹Species are pooled.

TABLE 9. TOTAL NUMBER OF INDIVIDUAL VOLES CAPTURED AT THE FENCE DURING EMIGRATION EXPERIMENTS. Captures from all experiments at each density, and for each treatment are added together.

		Control		Experimental	
		4 voles/ enclosure	8 voles/ enclosure	4 voles/ enclosure	8 voles/ enclosure
Meadow vole	♂	5	11	8	16
	♀	5	12	2	11
	all	10	23	10	27
Montane vole	♂	3	5	6	9
	♀	13	14	9	16
	all	16	19	15	25

this are very similar to the average number of captures. There were no significant differences in the number captured between experimental treatments and control treatments for either species at either density.

The number of individual montane voles captured was not significantly greater than the number of meadow voles at either density, but I feel that at the density of four per enclosure that these statistics are misleading. There is a 60% difference in captures in control treatments and a 50% difference in captures in experimental treatments between the two voles which is consistent with other factors indicating that the habitat in the enclosures was less suitable for montane voles.

The effect of density upon numbers of voles captured at the periphery was different for meadow voles than montane voles. A chi-square value of 12.01, $df = 1$, ($P < 0.01$) indicates that statistically significantly more meadow voles in both control and experimental treatments

were captured at a density of eight per enclosure than four per enclosure. More montane voles were captured at the periphery at the higher density than at the lower density, but the difference was not significant.

Survival Rates

Survival rates were calculated for each species by dividing the number of voles alive at the end of the second density of each experiment by the cumulative number of voles placed in each enclosure. There were no statistically significant differences in average survival rates between control and experimental treatments for either species (Table 10). Although these differences are slight and insignificant, it is

TABLE 10. AVERAGE SURVIVAL RATES FOR ALL EMIGRATION EXPERIMENTS.

Survival is presented as the percentage of animals remaining in the enclosures at the end of the second density of each experiment.

		Control	N	Experimental	N	t
Meadow vole	♂	68.3	32	68.7	32	
	♀	62.3	32	78.1	32	
	all	65.0	64	73.4	64	0.69
Montane vole	♂	60.4	32	50.0	32	
	♀	80.9	32	60.4	32	
	all	70.6	64	55.2	64	0.35

interesting that meadow vole survival is higher in experimental treatments while montane vole survival is higher in control treatments.

Also, most of the differences in survival rates between control and experimental treatments occur with females.

Weight Changes

Weight changes were calculated only for those voles that were placed in the enclosures at a density of four per enclosure and removed at the end of the experiment. Table 11 shows the average weight changes

TABLE 11. AVERAGE WEIGHT CHANGES IN GRAMS DURING EMIGRATION EXPERIMENTS. The time period was eight days.

		Control	Experimental	N	t
Meadow vole	♂	0.2 g	2.1 g	25	0.89
	♀	1.7 g	2.5 g	24	0.29
Montane vole	♂	-0.8 g	-1.8 g	18	1.01
	♀	-0.6 g	-0.2 g	25	0.25

for both species by sex and both treatments. Neither species demonstrated significantly different weight changes between control and experimental treatments.

Deaths

During the course of the emigration experiments four voles, two males and two females, were found dead in the peripheral area adjacent to the fence. During the telemetry experiments three voles were found dead near the fence. In both series of experiments these dead animals had been lacerated rather severely. In three of the cases in the

emigration experiments the dead animals had been previously captured in the peripheral traps. Although I did not see any of these animals being killed, I assume that they were killed by other voles. All of this mortality occurred in enclosures containing meadow voles only. If this type of mortality occurred during the other treatments, it occurred away from the periphery where I was unable to find the carcasses.

Trap Lines

From April, 1972, to January, 1973, a total of 56 meadow voles, 51 montane voles and 70 deer mice were captured in the trap lines east of the enclosures. Figure 3 shows the cumulative number of rodents captured during this time period. Populations of both meadow voles and montane voles increased in late spring and early summer. Numbers in both populations of voles leveled off by June and decreased through late summer and fall. The lack of captures of new individuals during December and January may have been due to snow reducing the availability of traps to rodents.

During every month that both species of voles were captured, individuals of both species were captured in trap line D in the bottom of the coulee. Figure 4A shows the total number and percentage of each species captured in each trap line. Though the distribution of captures of each species differed according to individual trap lines, both species were captured in all trap lines. A two-by-four

Figure 3. Cumulative number of rodents captured in four trap lines.

Figure 4. Number and distribution among four trap lines of captures of voles according to (A) which trap line the captures occurred in and (B) in which cover class captures occurred. Cover classes were designated according to density of cover and depth of litter.

contingency test of the number of captures of both species of voles in all trap lines ($X^2 = 24.26$, $df = 4$, $P < 0.01$) indicates that the distributions of captures of the two species were statistically significantly different in relation to the four trap lines.

Differences in vegetation selected by meadow voles and montane voles were estimated by two procedures. In the first procedure, 13 Daubenmire vegetation plots similar to those taken in the enclosures were placed along each trap line, and I considered these to be representative of each line. The vegetation selected by a vole was considered to be the same as that described along the line in which it was captured. The frequencies and coverage of plant species along each trap line are presented in Appendix Table 13. I consider the vegetation in the two trap lines (A and D) in which the largest numbers of voles were captured to differ significantly, because of the total of 22 species of plants found in these two lines only three were found in both lines.

Since meadow voles were captured in the four trap lines in significantly different ratios than montane voles and the plant species compositions were different along the two rows, A and D, in which most voles were captured, I consider the two species to have each selected different vegetation.

The second procedure of estimating vegetation selection was by determining the number of captures in vegetation of each of my four

cover classes (Figure 4B). A chi-square value of 30.98, $df = 4$, ($P < 0.01$) indicates that meadow voles were captured in the four cover classes in significantly different ratios than montane voles. Though most captures of both species of voles were in cover class four, more captures of montane voles than meadow voles were in the other three cover classes. Data from the trap lines indicates not only a difference in types of vegetation selected by each species of vole, as indicated also in the telemetry experiments, but a broader range of tolerance to cover differences by montane voles.

DISCUSSION

Several factors in the spatial activities of meadow voles and montane voles indicate that there may be some social interactions between the two species. Some significant differences between single species treatments and double species treatments were found in average home range sizes, overlap in home ranges, and the distances between individuals located during the same tracking run. A difference in vegetation selected by montane voles between single and double species enclosures was also found to be significant.

Montane voles demonstrated significantly larger home ranges in single species groupings as compared to groupings of both species. This could be accounted for by either social interactions or differences in habitat preferences or some combination of both. If meadow voles were dominant over montane voles and excluded montane voles from certain areas of habitat as suggested by Murie (1971), then a larger average home range of montane voles in the presence of meadow voles may be due to montane voles having to move farther to avoid areas occupied by meadow voles. In other words, the home range of montane voles may have to be larger to compensate for areas made unavailable to them by the presence of meadow voles.

The higher percentage of intraspecific home range overlap demonstrated by montane voles, the closer intraspecific spacing of individual montane voles, and the difference in vegetation selection

between single and mixed species groups demonstrated by montane voles support the concept of meadow vole dominance with montane voles avoiding them or areas occupied by them. These data indicate that the intraspecific tolerance of montane voles is significantly greater than their interspecific tolerance of meadow voles and that this affects their spatial arrangements and vegetation selection.

Meadow voles also demonstrated changes in home range size, overlap in home range, and distances among individuals similar to the changes demonstrated by montane voles. Though two out of three of these differences were statistically insignificant, they indicate that montane voles may have some small effect on the movements of meadow voles.

An alternative explanation of observed changes in movements of montane voles may lie in intraspecific competition for a limited amount of preferred vegetation. When montane voles were placed in enclosures with meadow voles the montane vole density per unit of preferred montane vole habitat was two. When montane voles were in enclosures alone the density was four voles per unit of preferred habitat. Thus, the smaller home ranges, the overlap, and closeness of individuals may have been due to an increased number of montane voles crowding into an unchanged amount of available preferred habitat.

Intraspecific crowding as an explanation of observed differences, however, is probably not valid for the following reasons. First, if montane voles were crowding into limited preferred habitat when there

were four per enclosure, then the vegetation selected during runs when only montane voles were in an enclosure should be fairly similar to that selected when in the presence of meadow voles. This is not the case, as indicated by significant differences in montane vole selection between control and experimental treatments. Secondly, in an intra-specific crowding situation one would expect voles to be located in more diverse vegetation types in single-species than in two-species groupings. If the number of species of plants measured near locations of voles is an indication of diversity of vegetation selected by montane voles, then the opposite of this is true. In three out of four enclosures, fewer species of plants were found in plots near locations of montane voles in single species treatments than when they were in the presence of meadow voles (Appendix Table 12). It appears that montane voles occupied a more diverse habitat in the presence of meadow voles, and when alone, montane voles possibly utilized fewer species in more preferred vegetation types. Conversely, the larger number of species of plants found in plots near locations of montane voles when they were in the presence of meadow voles may indicate that meadow voles were forcing montane voles to use more diverse, possibly less preferred habitat.

The reasons for montane voles appearing subordinate in the experimental enclosures could be explained in any of three ways. 1. Meadow voles are naturally dominant over montane voles as suggested by Murie

(1971), which could be the result of their higher population density as suggested by Krebs, *et al.* (1973). 2. The habitat in the enclosures was not optimal for montane voles, and they were less secure than meadow voles. This is supported by the montane voles' tendency to lose weight in the enclosure in both control and experimental treatments of the emigration experiments and also by the higher emigration rates of montane voles as compared to meadow voles. 3. Broader habitat tolerances of montane voles, as discussed below, may have enabled them to adjust to meadow voles. Probably a combination of all three is responsible for montane voles appearing subdominant.

Although an interspecific interaction was present between montane voles and meadow voles, its importance in maintaining habitat separation seems to be limited. In south central Montana the two species may coexist in the same local sites (Hodgson, 1972). No clear-cut habitat separations are apparent as Findley (1951, 1954) found in Wyoming, and if there is a dominance-subordination relationship between the two species, it is not strong enough to invariably segregate them into different habitats as in the instance cited by Koplin and Hoffmann (1968).

No significant shifts in centers of activity of either species were observed when experimental enclosures were converted from two-species to single-species systems during the telemetry experiments. This indicates that if an interspecific interaction was present it was not so

intense that it could keep individuals of either species entirely away from an area they might otherwise occupy. The results of the emigration experiments also indicate that interaction or direct competition was of rather low intensity, since the presence of both species of voles had no significant effect on the emigration rates of either.

Habitat preferences, as inferred from the vegetation analysis in the enclosures and on the trap lines, were different for each species of vole. Vegetation selection in the enclosures was shown by meadow voles in the experimental treatments and by montane voles in both control and experimental treatments. The fact that montane voles were selective in all treatments may indicate that the vegetation in the enclosures was less suitable for them. The chi-square analysis comparing vegetation selected by meadow voles with that selected by montane voles indicated that their preferences were different. There was probably little competition for vegetation at a population density of four per enclosure, which may in turn explain the low intensity of the interspecific interaction.

Although the preferred plant species of meadow voles and montane voles were not clear in either the tracking experiments or the trap lines, the differences in cover tolerances were clearly defined on the trap lines and indicated that meadow voles had a narrower range of tolerance than did montane voles. Both species preferred cover class type four (dense grass, soil not visible, and litter layer deeper than

10 cm), but montane voles were found more often than meadow voles in the other less dense cover types. Hodgson (1972) found similar cover tolerances for these two species in a diversity of habitats in the same area. This broader range of cover tolerance and possibly plant species tolerance may permit montane voles to inhabit different habitats when meadow voles are present than they would if alone. A greater flexibility in habitat utilization was also inferred by the telemetry experiments when montane voles demonstrated significantly different vegetation selections when alone than in the presence of meadow voles.

In this study area the mechanism segregating meadow voles and montane voles into their respective habitats seem to be a combination of interspecific social interaction and divergent habitat preferences. The social interaction is of minor importance and acts to limit the movements of montane voles but does not exclude them from the area as long as the habitat is favorable. The difference in habitat preferences of these two species is probably the most important factor separating the two. By all vegetation analyses employed in this study, meadow voles demonstrated preferences that were significantly different from montane voles. These differences were similar to those described by Hodgson (1972) and showed meadow voles to be restricted to very dense vegetation with montane voles having similar preferences for heavy cover but broader tolerances of mesic and dry sites with less cover.

I think that the relative importance of social interaction and habitat preferences may change along a gradient of habitats with social interaction becoming more important as the gradient approaches a point of uniform optimal habitat for meadow voles. Interaction between the two species probably results in meadow voles occupying areas of preferred habitat with montane voles avoiding these areas. If the overall habitat is diverse enough in a local area, the montane voles can remain in the area by using habitat types not used by meadow voles. In habitats that approach uniformity of meadow vole habitat, montane voles are excluded. All of the proximate factors involved in maintaining habitat separations suggested by Koplin and Hoffmann (1968) and Hodgson (1972) are probably active, but the importance of each changes along a habitat gradient. If relatively large continuous areas of preferred meadow vole habitat are present, the effects of interspecific competition in segregating the two species into their respective habitats as suggested by Findley, (1954) and Getz (1962) become obvious. This is strongly indicated by Koplin and Hoffmann (1968) when montane voles entered a section of limited but uniform meadow vole habitat only after the meadow voles were removed. In areas of a mosaic nature containing habitat suitable for both species, habitat preferences as suggested by Hilden (1965), Wecker (1963) and Harris (1952) are sufficiently different to allow the two species to avoid competition by using separate though intermixed, habitats. The apparent effect of social interaction

becomes less obvious in this case, because areas from which montane voles are excluded are intermixed in a mosaic with those areas from which they are not excluded, and the two species cohabit the area.

To conclude, I feel that combinations of factors, specifically interspecific social interactions and divergent habitat preferences, are active in spatially segregating meadow voles and montane voles, but the relative importance of each changes with the composition of the habitat in which the voles are found.

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APPENDIX

TABLE 12. VEGETATIVE COMPOSITION OF THE FOUR ENCLOSURES. Frequency and coverage classes were calculated according to Daubenmire's (1959) method and were taken from 81 plots placed in a regular two meter grid in each enclosure.

	Enclosure 1		Enclosure 2		Enclosure 3		Enclosure 4	
	Fre-	%	Fre-	%	Fre-	%	Fre-	%
	quency	age	quency	age	quency	age	quency	age
Grasses								
<i>Agropyron repens</i>	26	4	43	3	64	12	53	6
<i>Phleum pratense</i>	3	t*	9	t	27	t	23	t
<i>Poa pratensis</i>	100	93	98	91	100	87	99	93
Forbs								
<i>Achillea millefolium</i>	--	--	3	t	1	t	--	--
<i>Artemisia ludoviciana</i>	41	3	43	2	23	1	38	4
<i>Balsamorhiza sagittata</i>	1	t	0	0	--	--	1	t
<i>Cirsium arvense</i>	--	--	--	--	31	2	22	2
<i>Erigeron divergens</i>	17	1	35	1	17	t	21	1
<i>Lactuca serriola</i>	--	--	--	--	4	t	3	t
<i>Gaura coccinea</i>	--	--	1	t	--	--	--	--
<i>Geranium viscosissimum</i>	22	1	20	1	12	1	10	t
<i>Solidago missouriensis</i>	10	t	14	t	11	t	1	t
<i>Thlaspi arvense</i>	--	--	1	t	1	t	--	--
<i>Tragopogon dubius</i>	--	--	3	t	6	t	1	t
Shrubs								
<i>Rosa woodsii</i>	69	15	42	9	49	8	53	5

*Trace

TABLE 13. VEGETATIVE CHARACTERISTICS OF FOUR TRAP LINES AS DETERMINED BY 13 REGULARLY PLACED 2 X 10 dm DAUBENMIRE PLOTS ALONG EACH TRAP LINE. Line A is at the crest of the coulee, line D is in the bottom, and lines B and C are one-third and two-thirds the way down the slope from line A, respectively.

	Line A		Line B		Line C		Line D	
	Fre- quency	Cover- age %	Ere- quency	Cover- age %	Fre- quency	Cover- age %	Ere- quency	Cover- age %
Grasses								
<i>Agropyron repens</i>	69	20	92	12	61	3	69	15
<i>Bromus tectorum</i>	38	64	--	--	--	--	--	--
<i>Hordeum jubatum</i>	23	5	46	1	38	1	--	--
<i>Poa pratensis</i>	31	6	23	t*	8	t	61	20
Forbs								
<i>Achillea millefolium</i>	8	t	8	1	8	t	--	--
<i>Agoseris glauca</i>	15	1	--	--	15	t	15	t
<i>Alyssum allysoides</i>	--	--	--	--	92	2	--	--
<i>Artemisia ludoviciana</i>	--	--	77	5	23	t	15	t
<i>Astragalus drummondii</i>	--	--	--	--	8	t	--	--
<i>Besseyia wyomingensis</i>	--	--	--	--	--	--	8	t
<i>Brodiaea grandiflora</i>	--	--	--	--	--	--	8	t
<i>Cirsium arvense</i>	--	--	--	--	--	--	15	8
<i>Cirsium undulatum</i>	--	--	--	--	23	2	23	t
<i>Collomia linearis</i>	--	--	--	--	--	--	8	t
<i>Gaura coccinea</i>	--	--	15	t	69	3	--	--
<i>Geranium viscosissimum</i>	--	--	--	--	--	--	15	t
<i>Geum triflorum</i>	--	--	--	--	--	--	15	t
<i>Linum perenne</i>	--	--	--	--	8	t	--	--
<i>Lithospermum arvense</i>	15	3	8	2	23	t	--	--
<i>Lithospermum ruderales</i>	38	8	23	2	--	--	--	--
<i>Lupinus sericeus</i>	8	1	--	--	--	--	--	--
<i>Phlox hoodii</i>	--	--	8	t	15	t	--	--

TABLE 13. (Continued).

	Line A		Line B		Line C		Line D	
	Fre- quency	Cover- age %	Fre- quency	Cover- age %	Fre- quency	Cover- age %	Fre- quency	Cover- age %
Forbs (Continued)								
<i>Phlox longifolia</i>	--	--	31	t	15	t	--	--
<i>Taraxacum officinale</i>	8	t	--	--	--	--	--	--
<i>Thlaspi arvense</i>	38	4	--	--	--	--	--	--
<i>Tragopogon dubius</i>	--	--	8	t	23	t	--	--
<i>Vicia americana</i>	--	--	--	--	--	--	8	t
<i>Vicia villosa</i>	--	--	--	--	--	--	8	t
Shrubs								
<i>Rosa woodsii</i>	--	--	--	--	--	--	31	t
Litter	100	83	100	27	100	25	100	95
Total		136		56		40		140

*Trace`

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