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INVESTIGATIONS OF HABITAT SEGREGATION IN MICROTUS
IN WESTERN MONTANA

by

JAN O. MURIE

B.S. Colorado State University, 1959

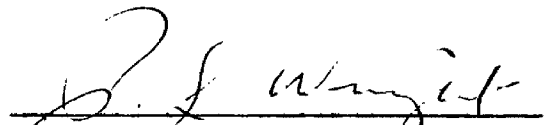
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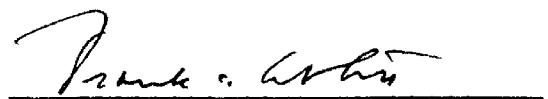
Master of Arts

MONTANA STATE UNIVERSITY

1963

Approved by:


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ACKNOWLEDGMENTS

I would like to express my gratitude to Dr. R. S. Hoffmann, who formulated this problem and offered many helpful suggestions throughout the study. I am grateful to Dr. P. L. Wright, chairman of my examining committee, for providing guidance in the preparation of the manuscript and encouragement during the study.

I also want to thank the other members of my examining committee, Dr. E. W. Pfeiffer and Dr. S. J. Preece, Jr., for useful comments on the manuscript. Other members of the Zoology Department staff and graduate students also provided helpful suggestions concerning certain aspects of the study.

Dr. C. L. Larson permitted me to use a room for housing the artificial habitat and offered several useful suggestions.

Mr. C. J. Henry, manager of the National Bison Range, kindly allowed me to conduct field work on the Bison Range and furnished overnight accommodations while field work was in progress.

The Co-operative Wildlife Unit at Montana State University reimbursed me for travel expenses for the field work.

I also want to express my appreciation to the following people: Dr. H. E. Reinhardt and Dr. J. C. Holmes, for assistance with the statistical treatment of data; Mr. J. R. Koplín, for providing me with much information about the problem and the study areas on the National Bison Range; Dr. R. D. Taber and Mr. J. Sullivan, for valuable criticisms of the manuscript; Mr. D. Lawrence,

for advice on the recording system for the artificial habitat; and Dr. W. J. Griffiths, Jr., for helpful discussions of some aspects of the study.

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INTRODUCTION

Several workers in the field of microtine biology (Findley, 1951; Warren, 1942; Hall, 1946) have stated that in areas where the range of Microtus pennsylvanicus and M. montanus overlap, the former species is relatively restricted to wet habitat and the latter is most commonly found in drier areas. In areas where the ranges of these two species do not overlap, they may occupy both dry and wet habitat. Findley (1954) suggested that the presence of M. montanus forces M. pennsylvanicus to retreat to wet habitat and that this restriction of M. pennsylvanicus to its presumably optimum niche may be at least partially due to competition between the species.

Acting on Findley's proposal that this habitat segregation might result from competition, Koplín (1962) inferred that "...artificial reduction of meadow voles (M. pennsylvanicus) in a hydrosere will result in movement of montane voles (M. montanus) into the vacated niche." Koplín carried out a field experiment to test this hypothesis and found that the reduction of M. pennsylvanicus in mesic habitat did bring about the invasion of that habitat by M. montanus. However, the movements of the montane voles into the mesic areas were of a transitory nature and circumstances prevented continued trapping to determine if the immigrating animals would establish movement patterns or centers of activity within the wet habitat. Appraisal of Koplín's trapping data did indicate that these species "...avoided rather than competed for mutually shared habitat...."

Since Koplin's study revealed that direct spatial competition between M. pennsylvanicus and M. montanus is probably temporary or non-existent, their habitat segregation must be controlled by some other factor or combination of factors. This study was designed to test two factors which might operate in preventing interspecific competition and to continue reduction of M. pennsylvanicus in the mesic habitat to determine if M. montanus would permanently occupy that habitat.

Since soil moisture was one of the most obvious differences between the two habitat types, it was felt that a soil moisture preference of one or both species might be important in maintaining their habitat segregation. To determine if any preferences existed an experiment involving artificial habitats, one with wet soil, the other with dry, was designed so that individual voles were presented with a choice of the two substrates.

Comparative studies of this sort on habitat selection of rodents have been done by Harris (1952) and Wirtz and Pearson (1960). Harris worked with two subspecies of the deermouse, Peromyscus maniculatus, and Wirtz and Pearson experimented with Microtus pennsylvanicus and Peromyscus leucopus. The artificial habitats in both these studies simulated vegetational types.

From Koplin's conclusion that M. pennsylvanicus and M. montanus avoid rather than compete for mutually shared habitat, it might be inferred that interspecific agonism is important in reducing or preventing active competition for niche factors. If this inference were correct, it might be expected that agonistic behavior would be more severe between species than between individuals of the same species. To

test this hypothesis, a series of observations on interactions between pairs of voles was made. Getz (1962) conducted similar studies on aggressive behavior of meadow voles (Microtus pennsylvanicus) and prairie voles (M. ochrogaster). King (1957) compared intra- and inter-specific aggressive behavior of house mice (Mus musculus) and deer mice (Peromyscus maniculatus), and Wirtz and Pearson (1960) made observations on aggressive behavior exhibited by Microtus pennsylvanicus and Peromyscus leucopus.

METHODS AND MATERIALS

Field Experiment

Field work was carried out on the National Bison Range, a big game refuge in western Montana administered by the U.S. Bureau of Sport Fisheries and Wildlife. The area trapped was the 2.58 acre experimental trap grid laid out and used by Koplin (1962). The grid encloses a small pond with associated mesic vegetation and includes portions of the surrounding dry grassland. Sedge (Carex) and cattail (Typha) predominate in areas of standing water and watersoaked soil, blue grass (Poa sp.) occurs in damp to muddy soil and palouse prairie vegetation as described by Mitchell (1958) is found in the relatively dry soil (see Koplin's thesis for vegetational maps and more detailed description of the area). The trapping stations were marked with yellow bridge spikes spaced at 25-foot intervals. Hardware-cloth drift fences constructed by Koplin were in place at each end of a small stream running through the grid plot and several live traps were set along these two fences. This precaution was taken to reduce the amount of immigration into the trapping plot by M. pennsylvanicus.

The box-type live traps were constructed from 1/4-inch fiber board after the design described by Mosby (1955). Trap doors were made of 1/16-inch sheet aluminum or tin. A mixture of peanut butter and rolled oats was used for bait and traps were provided with nonabsorbent cotton for nest material.

Live trapping was carried out intermittently from July 19 to October 3, 1962. From 49 to 63 traps were set at each trapping period and these were placed only at stations in or immediately adjacent to the mesic habitat. All M. pennsylvanicus captured were removed from the area and M. montanus captured were marked and released. Marking was by ear tagging with numbered stainless steel fingerling tags and the toe clipping method described by Baumgartner (1940). Other species trapped were released at the point of capture. Specific identification of the captured voles was done on the basis of differences in pelage and foot color between the two species (Hall and Kelson, 1959). Criteria set forth by Davis (1956) were used to distinguish sexes.

During the hot summer months, the traps were exposed only at night to reduce vole mortalities from overheating. In September and October when the days were cooler, traps were set both day and night and checked near sundown and sunrise.

Experimental Animals

Nineteen Microtus pennsylvanicus, 10 females and 9 males, and 29 M. montanus, 18 females and 11 males, were kept in the laboratory for use in the habitat selection and vole interaction experiments. Nine other voles died after a short time in captivity. Ten of the experimental voles were captured on the National Bison Range, two in the spring of 1962, eight during September and October, 1962. The remaining 38 voles were trapped in the vicinity of Missoula during October, November, and December, 1962. Five M. pennsylvanicus were caught by hand near Missoula in April, 1963.

Eighteen M. pennsylvanicus and 22 M. montanus were used in the habitat selection experiment. Thirteen of each species, 8 males and 5 females, were used in the vole interaction trials. Only voles that lived in isolation were used in interaction trials. All individuals were in captivity at least 2 to 3 months before being used in the experiments so all were sexually mature.

The voles were kept in 24" x 18" x 16" wire cages for most of the duration of captivity. Each cage had a central partition making two separate 12" x 18" x 16" compartments. The cages were set side by side on three-tiered racks. Only one vole was kept in a single compartment except in three cases where there were two voles per compartment. Each compartment was furnished with nest material (cotton, paper strips, shredded wood or burlap), a food dish, and either a water dish or a bottle water dispenser. The voles subsisted on an ad libitum diet of Purina rabbit chow and fresh lettuce. Some voles were temporarily kept in plastic pans measuring 20" x 4" x 10" and glass jars, 8" deep and 7" in diameter. One to three inches of shavings covered the bottom of these containers and perforated tin lids covered them. Food dishes and water bottles were furnished as in the wire cages.

The caged voles were kept in a small room in the basement of the Health Science Building on the Montana State University campus. A variety of other animals were also kept in the room at various times and voles were exposed to a large amount of human activity in the room. Some voles became relatively oblivious to activity in the room and were even quite bold. Others were shy and secretive and never did seem to become accustomed to humans.

All captive voles were toe clipped according to the method described by Baumgartner (1940).

Voles were removed from the cage by two methods. Usually a wire screen cone about 8 inches long with a diameter of 3 inches at the open end was inverted over a vole. The vole then moved spontaneously or was chased toward the closed end of the cone and the open end was squeezed shut. Less often voles were caught by hand using gloves. The wire cone method was much more efficient and the voles could be moved in and out of their cages without seeming to become greatly frightened.

Habitat Selection Experiment

The artificial habitat was set up in one corner of a basement animal room in the Health Science Building on the Montana State University campus in Missoula, Montana. Cages containing white mice and rabbits belonging to the Stella Duncan Memorial Institute occupied the remainder of the wall space in the room (see Figure 1). Some features of the artificial habitat and the criteria used to determine habitat preferences were adapted from Harris (1952).

The habitats were housed in a 4' x 8' enclosure made of low grade 1" x 16" boards. A partition, also of 1" x 16" board, divided the compartment into two equal sections. A passageway 4 inches wide was cut in the center of the partition. This enclosure was set on a platform of 1-inch scrap lumber covered with a layer of black rolled plastic material to protect the floor from dampness. Two to three inches of soil, very fine sandy loam, was spread evenly over the floor of the enclosure. Slabs of cardboard were tacked onto the outside of the

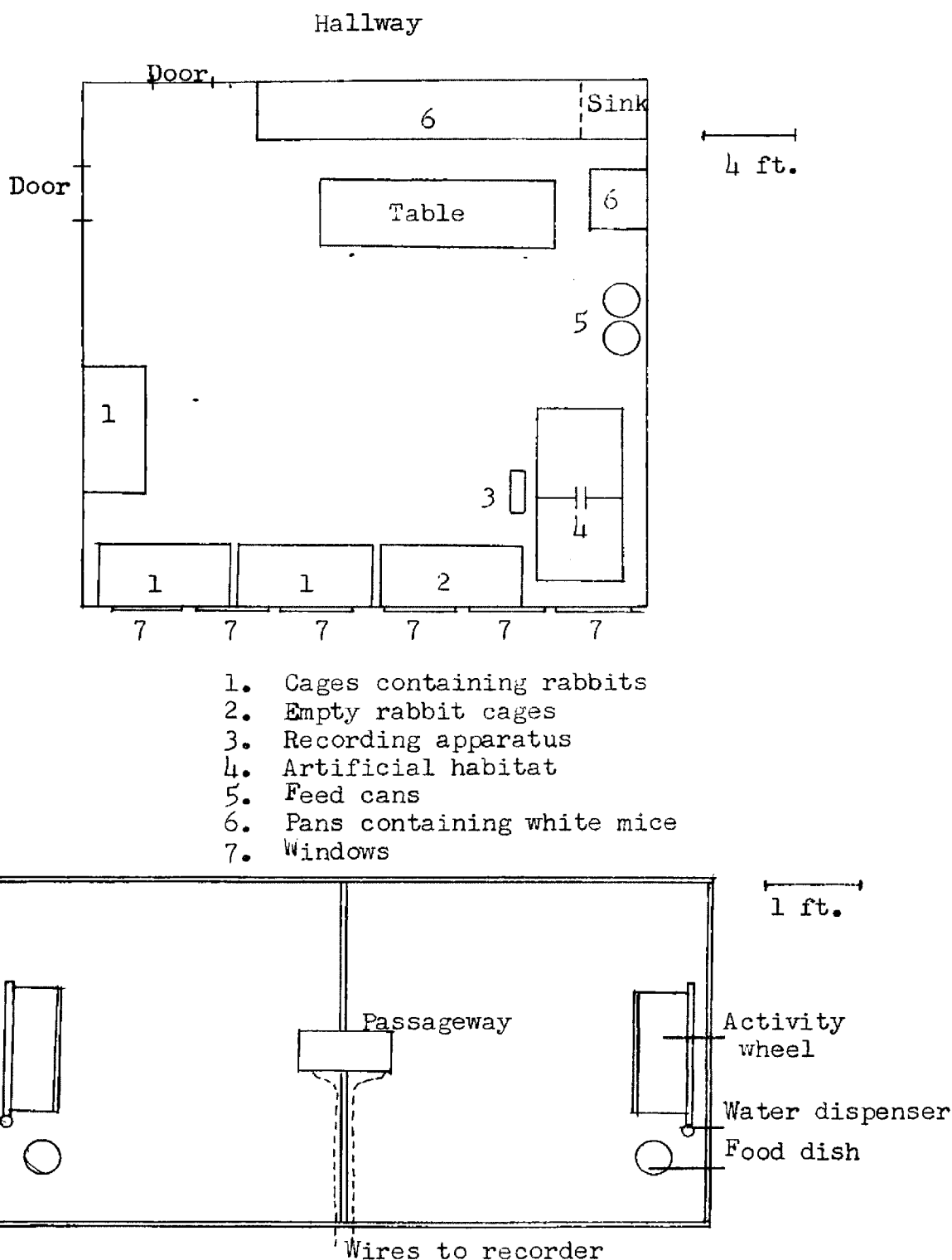


FIGURE 1

Top: Diagram of room containing artificial habitat as viewed from above.

Bottom: Diagram of artificial habitat as viewed from above.

enclosure extending about 14 inches above the board walls, thus making the total height of the walls approximately 30 inches.

A rat-size activity or exercise wheel, food dish, and water dispenser were placed in corresponding positions in both of the compartments. The soil in one compartment was kept moist to the touch by sprinkling water on it periodically throughout the experiment, and the other was allowed to remain dry. Subjective judgment was used in keeping the moisture in the wet habitat fairly constant. Rewetting the soil every two or three days seemed to provide adequate moisture. No standing water was present in the wet soil habitat while the enclosure was occupied by a vole.

Black rolled plastic material supported by a wooden framework covered the entire enclosure while occupied by a vole, both day and night. The material was held suspended approximately 42 inches above the dirt substrate and, with help from the walls on two sides, excluded light from all sides of the area as well as the top.

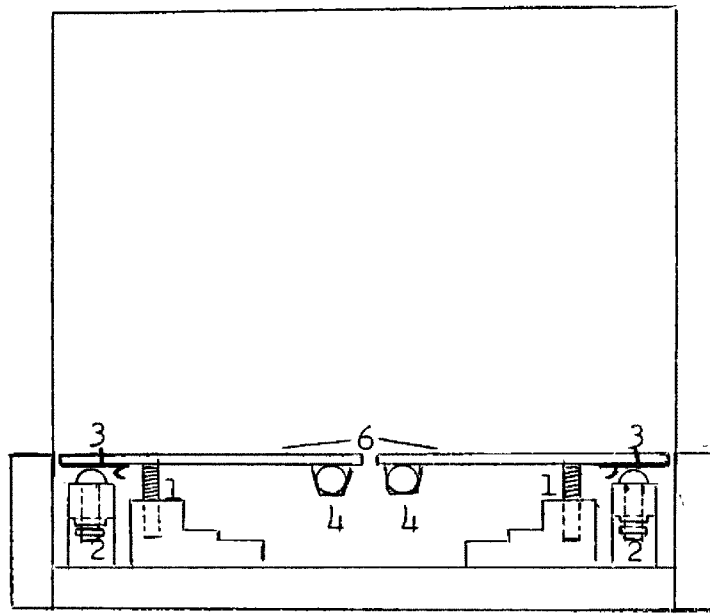
The habitat preferences of the voles were measured by four methods: (1) amount of food consumed or taken from dish; (2) amount of water consumed; (3) number of activity wheel revolutions; and (4) total time spent in each compartment.

Before each trial, about 30 grams of Purina rabbit chow pellets were put in the fingerbowl size crockery food dishes and each dish, with its contents, was weighed. By weighing the food dishes after the trial, the amount of food taken from the dish could be determined. No effort was made to determine the amount of food taken from the dish but not consumed.

Water dispensers consisted of a glass tube, $3/16$ inch in diameter and 24 or 36 inches long, with 3- to 4-inch sections of rubber tubing at each end. Attached to the tubing at the lower end was a steel tube from a standard bottle water dispenser with a constricted opening at one end. The upper tube was pinched off with a hose clamp. The level of water in the glass tube was measured at the beginning and end of each trial and the differences between these readings was recorded in centimeters. Previously, the volume per unit length for the glass tubes had been determined so the measures in centimeters could be converted to units of volume.

Activity wheels were equipped with counters which were read before and after each trial. The latter reading minus the former yielded the number of revolutions for the trial. Many of the voles had previously been exposed to an activity wheel but some had not. Some voles may not have used the activity wheels much due to their inexperience with them. In many cases, however, voles used the wheels readily without previous experience.

In the passageway between the two compartments, a treadle system was installed, the treadles being on the same level as the soil of the habitats (see Figure 2). The system's framework, constructed of $3/4$ -inch boards, consisted of: (1) a baseboard, 5" x 10 $1/2$ ", lying lengthwise in the gap in the partition between the habitats; (2) a board extending along each side of the baseboard, 12 inches high and perpendicular to the floor; and, (3) boards at each end of the baseboard, 3 inches high and perpendicular to the floor. Within this box-like structure, two fiberboard treadles were attached to steel rods located at either side



- 1. Spring
- 2. Brass screw
- 3. Copper plate
- 4. Brass rod
- 5. Wires leading to recorder
- 6. Treadle

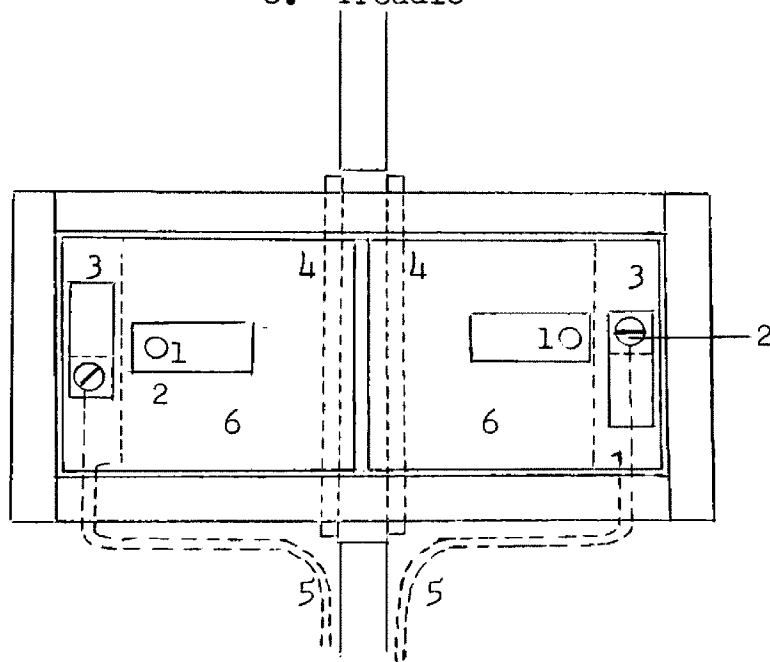
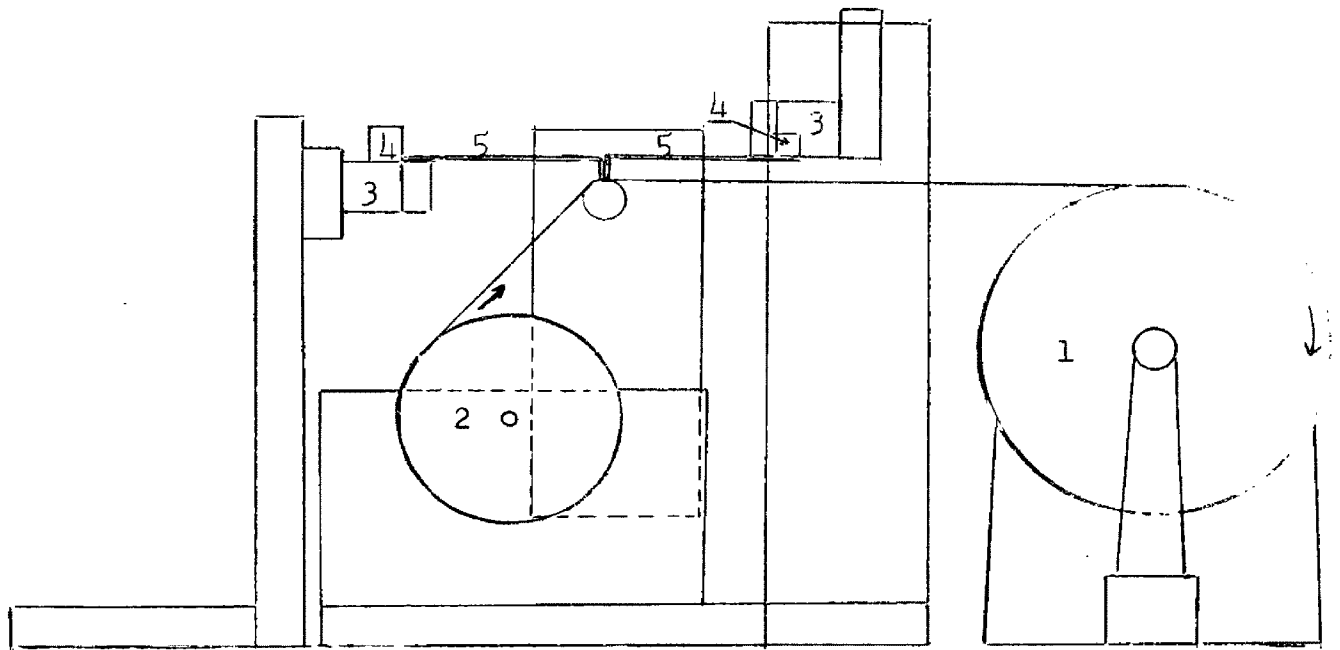


FIGURE 2

Diagrams of treadle system used in artificial habitat,
reduced to $\frac{1}{4}$ actual size.
Side view above, top view below.

of but close to the center of the framework. Each treadle was supported at its unattached end by a small coil spring with the lower portion set in a block of wood for support. In this way the two treadles were held about 2 inches above and horizontal to the baseboard level with the end-walls of the frame and the dirt in the two compartments. A copper plate on the bottom side of each treadle contacted a brass bolt attached to a block of wood on the baseboard whenever a treadle was slightly depressed. Wires led from each copper plate and brass bolt through the sides of the treadle framework, under the soil, along the partition between compartments, and through a hole in the compartment wall to the recording apparatus outside the compartment. Between the walls at each end of the passageway, a piece of cardboard was inserted leaving spaces about one inch high between the bottoms of the cardboard and the treadles. This arrangement of cardboard prevented voles from going through the passageway without depressing the treadles sufficiently to activate the circuits.

The recording apparatus (see Figure 3) consisted of a two-piece, wooden framework with a Series 200 Guardian relay mounted on each part. A kymograph ink pen with ink cup was glued to the contact assembly of each relay. The two framework structures were then placed together so the ink pens faced each other and the downward-turned writing tips were side by side. A roll of adding machine tape, 3 inches wide, was placed on a metal rod axle, supported by the side walls of the framework, below the level of the relays and pens. The tape was drawn over a cross-bar on which the pen tips rested and thence beyond the framework to an electric kymograph lying on its side. During the course of a trial,



- 1. Kymograph drum
- 2. Paper roll
- 3. Guardian relay
- 4. Ink well
- 5. Ink pen

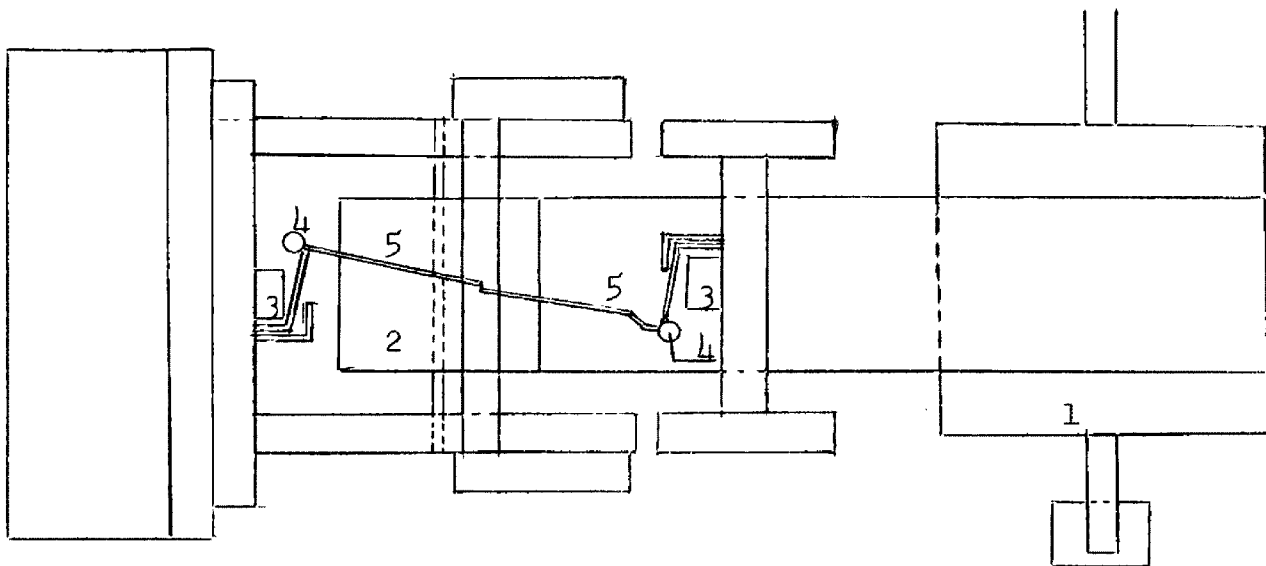


FIGURE 3

Diagrams of recording apparatus, reduced to $\frac{1}{4}$ actual size.
Side view above, top view below.

the kymograph was turned on at its slowest speed and drew the tape along beneath the recording pens.

The wires from one of the treadles and the associated bolt connected to the two poles of the relay, one of the wires first passing through a 6-volt dry cell battery. The other treadle, bolt and relay were connected in the same manner. When a vole stepped on a treadle, the circuit was completed, the electromagnetic coil in the relay was activated moving the contact assembly and the attached pen, thus causing a "blip" to appear on the tape. By noting which pen made the last blip on the tape, it could be determined to which compartment the vole had passed.

The speed of the tape varied somewhat during the course of a trial due to the increasing circumference of the drum as the paper was rolled onto it. This was partially compensated for by measuring the rate of the tape's movement near the beginning and the end of the trial and averaging the two values. Some variation may not have been eliminated by this procedure but probably not enough to greatly affect the results.

To begin a trial, measurements of food, water and activity wheel counters were recorded at 8 a.m. A vole was then introduced into the passageway between the two habitats so its initial habitat choice was made somewhat random, and the entire enclosure was covered with the black plastic material. The recorder was not put in operation at this time. Twelve hours later, about 8 p.m., the cover was removed, readings of food, water and activity wheel revolutions were made, the cover was replaced and the recording apparatus was put into action. The vole in the habitat was usually left undisturbed at this time, but occasionally

it was induced to go through the passageway twice to determine if the treadle system was adjusted properly. When this was done, the vole was in the same compartment after testing the treadle as it was beforehand. This first 12-hour period during the day allowed the vole to become familiar with both compartments so it would have a basis for "making a choice" during the second 12-hour period. The vole remained in the enclosure until 8 a.m. the next day and was then removed. Measurements of food, water and activity wheel revolutions were again made and the tape was removed from the recorder and analyzed. The rate of movement of the tape was measured when the recorder was first started at night and just before it was turned off in the morning. These two values were averaged to arrive at the converting factor from distance to time. By analysis of the tape, the total length of tape passing while the vole was on each side was determined, and these figures could then be converted from inches to minutes.

If it appeared that a vole may not have been in one of the compartments during the course of the trial or if a vole somehow escaped from the enclosure, data from that trial were not used.

On several occasions, malfunctioning of the treadle system or recording apparatus occurred and I was unable to determine the amount of time spent by the vole in either side. Whenever this happened, another trial was conducted with the same vole. However, data on food and water consumption and activity wheel revolutions were used for analysis even if the time spent in the compartments was not available for that trial.

When trials were begun, the south compartment held dry soil and the north compartment had a wet substrate. After each of the original experimental voles had been used in at least one trial with this arrangement, the substrates were switched so the south compartment was wet and the north one was dry. Each original vole then had at least one trial with this arrangement.

Vole Interaction Experiment

Observations were made on pairs of voles to determine what sort of agonistic reactions occurred between individuals and to see if a difference between inter- and intraspecific agonism existed. Trials were conducted in a small room in the Health Science Building basement, next to the room in which the voles were kept. Observations were made both during the day and at night. The room was not otherwise occupied so observations were made with fairly undisturbed conditions. Noises from the floor above and the basement hallway could be heard in the room but did not seem to have a significant effect on the animals under observation.

The observation cage was 16" x 8" x 8". The base and end walls were made of 3/4-inch laminated boards. Quarter-inch mesh screen formed the side walls. A removable cardboard partition divided the cage into two halves. The top was covered by 2 squares of glass when the cage was in use. About an inch of wood shavings were spread evenly on the cage floor and these were changed after every 5 or 6 trials.

The cage was set in the middle of the observation room about 3 feet from the floor during the trials. The room was lighted with overhead

fluorescent lights. All observations were made while sitting quietly on a chair placed 2 1/2 to 4 feet from the cage. Only in a few cases did it appear that my presence modified a vole's behavior to any extent.

To begin a trial, two voles were placed in the observation cage, one on each side of the partition, and the glass plates were placed over the top. The partition was not removed until both animals had calmed down, usually 2 to 5 minutes later. After removal of the partition, actions of the voles were noted and recorded for 10 minutes. The partition was then replaced and the voles were removed and replaced in their usual cages.

In recording the actions of the voles during a trial, most attention was given to the approaches of one to another and the reactions of both the approached and approaching individuals. Precise detailed descriptions of most activities were not made, but some general impressions were recorded.

Before each of the first few trials, Phipps & Bird blue kymograph ink was applied to the tail of one vole to aid in distinguishing it from the other animal under observation. This practice was discontinued after several trials when it was found that the two voles involved in a trial were quite easily distinguishable without the aid of extra marks.

No vole was used in more than two trials in one day and most were only used once a day. Whenever a vole was used twice in one day, the two trials were separated by at least 6 hours.

RESULTS

Field Experiment

Reduction of M. pennsylvanicus on the experimental plot on the National Bison Range was carried out through April, 1962, by Koplín. In order to gain further information concerning movements of M. montanus in the mesic habitat, I began trapping the same area in July, 1962.

During the period from July to October, 1962, 69½ trap nights and 25½ trap days resulted in captures of 103 Peromyscus maniculatus, 60 Sorex vagrans, 3 Mustela frenata, and the capture and removal of 40 Microtus pennsylvanicus. No M. montanus were captured.

At first glance, these data seem to indicate that the reduction of M. pennsylvanicus does not induce the movement of M. montanus into the partially vacated mesic habitat. This would be in direct opposition to Koplín's conclusion that invasion of the mesic habitat by M. montanus does take place. This apparent contradiction can be resolved by looking more closely at the condition of the vole populations during the two trapping periods.

Vole populations on the National Bison Range were quite high during the summer and fall of 1961 as indicated by Koplín's trapping success and the abundance of vole sign, such as grass cuttings, runways, and dropping stations (J. R. Koplín and C. J. Henry, personal communication). Population levels were still relatively high in the early spring of 1962, but numbers seemed to decline throughout the spring and summer. During the course of this study, little vole sign was

present in the vicinity of the experimental trapping plot or in other areas of the Bison Range where abundant sign of microtine activity had been seen the year before (C. J. Henry, personal communication). The difference in population levels becomes more apparent when one compares the yield rate of 0.14 voles per trap exposure during the preliminary phase of Koplin's trapping (June 23 to September 17, 1961) to the yield rate of .042 voles per trap exposure in this study.

It seems reasonable to assume that at high densities, pressure would be exerted on an animal population to invade all the suitable habitat available. Conversely, low densities would result in little or no pressure to occupy new territory. In view of the apparent low vole population at the time this trapping was conducted, it is concluded that population densities of Microtus montanus were not sufficiently great to cause them to invade the mesic habitat after reduction of the resident M. pennsylvanicus population.

Habitat Selection Experiment

Usable data were obtained from 90 trials of the habitat selection experiment, 51 with Microtus montanus, 39 with M. pennsylvanicus. Eighteen M. pennsylvanicus and 22 M. montanus individuals were used in the trials. Eight voles, 4 of each species, were used in only 1 trial. All others had at least 2 trials. For each trial, the amount of food and water consumed* and number of activity wheel revolutions were recorded for each habitat and for both the first (day) and second (night)

* Although the food measurement is a measure of food removed from the food dish rather than actual food consumed, reference will be made to food consumption for the sake of simplicity.

12-hour periods. These measurements were also converted to the percent of the total for each of the two habitats. The total time spent in each compartment was determined on a percentage basis. All four of these criteria were analyzed for each species to see if either vole utilized one of the two habitats significantly more than the other. The rank-sum test taken from Dixon and Massey (1957) was the statistic used in these determinations. The test was used for the actual values of food and water consumption and activity wheel revolutions and the percentage values for all four criteria used for determination of preferences. Tests were made on total values for the entire 24-hour duration of a trial as well as results from the second 12-hour period only. Significance of the results as determined by the rank-sum tests are presented in Table I, Columns 5 and 6.

Before examining the results in Table I, a short discussion of the relative merits of the four criteria used in determining habitat preferences is worthwhile. It is difficult to find an objective method of analyzing the criteria, but some subjective interpretations can be made.

The time spent in each habitat is an approximate measure of general activity and as such should be a relatively effective method of determining habitat preferences. Food consumption, since it is closely tied to a vole's daily activities, is probably also a fairly reliable measure.

The effectiveness of both water consumption and activity wheel revolutions as habitat preference measures are somewhat limited. Quite a number of the voles were never exposed to a water dispenser of the type

TABLE I

Mean values of habitat preference measurements and significance levels for the rank sum tests.

		<u>Col. 1</u>	<u>Col. 2</u>	<u>Col. 3</u>	<u>Col. 4</u>	<u>Col. 5</u>	<u>Col. 6</u>
		No. of trials	Mean amount in wet	Mean amount in dry	Mean amount for both habitats	Level of significance determined by rank sum test (actual values)	Level of significance determined by rank sum test (percentages of totals for both habitats)
<u>Microtus montanus</u>	Food, night	50	1.44 g.	0.94 g.	2.38 g.	99%	99%
"	Food, entire trial	50	3.04 g.	1.82 g.	4.86 g.	99%	99%
"	Water, night	51	1.08 ml.	2.34 ml.	3.42 ml.	99%	99%
"	Water, entire trial	51	1.89 ml.	3.85 ml.	5.74 ml.	99%	99%
"	Activity wheel revolutions, night	51	856	543	1399	62%	73%
"	Activity wheel revolutions, entire trial	51	1818	995	2813	77%	84%
"	Time, night	42	49.3%	50.7%	---	---	52%

TABLE I (continued)

		<u>Col. 1</u>	<u>Col. 2</u>	<u>Col. 3</u>	<u>Col. 4</u>	<u>Col. 5</u>	<u>Col. 6</u>
		No. of trials	Mean amount in wet	Mean amount in dry	Mean amount for both habitats	Level of significance determined by rank sum test (actual values)	Level of significance determined by rank sum test (percentages of totals for both habitats)
<u>Microtus pennsylvanicus</u>	Food, night	39	2.15 g.	0.99 g.	3.14 g.	99%	99%
"	Food, entire trial	39	3.90 g.	2.10 g.	6.00 g.	99%	99%
"	Water, night	39	2.36 ml.	2.13 ml.	4.49 ml.	83%	80%
"	Water, entire trial	39	4.00 ml.	3.76 ml.	7.76 ml.	56%	54%
"	Activity wheel revolutions, night	39	799	529	1328	87%	99%
"	Activity wheel revolutions, entire trial	39	1367	904	2271	91%	98%
"	Time, night	29	59.2%	40.8%	---	---	98%

present in the artificial habitats before their encounter with it in the habitats. It may have taken some time for these "naive" voles to learn how to get water out of the dispenser since no water was consumed in either habitat in ten trials and very little water was consumed in a number of other trials. It seems quite likely that a vole could have a tendency to continue drinking from the same water dispenser that it first used. If this is true, it would be possible for most drinking to take place in the less preferred habitat, since the initial water consumption probably occurred during initial explorations by the vole and thus might occur with about equal probability in either habitat. However, it must be kept in mind that a vole might also tend to seek out water in the preferred habitat. Since it was not clear which, if either, of these two phenomena occurred, it seems advisable to regard water consumption as somewhat unreliable in the determination of habitat preferences. The same case could conceivably be argued for food consumption but in this experiment, the food was much more readily available than water (open food dishes as opposed to hanging tube type water dispenser). Eating might also be considered as taking up more of a vole's time than drinking, and for that reason would be more closely correlated to total time spent in the habitats.

Of the four measures, the activity wheel was the least associated with the primary habitat variable, soil moisture. Although a vole might be more likely to enter the activity wheel in the preferred habitat, once it was in the wheel, the number of revolutions made might be more dependent on the vole's "desire" to exercise than on the nature of the substrate.

Harris (1952) used these same criteria in a series of 13 habitat selection experiments with two races of Peromyscus maniculatus. He estimated the effectiveness of these methods by the frequency with which the measurements revealed a statistically significant difference in artificial-habitat selection by the mice. From these estimations he found that food and water consumption appeared to be the best of the measures and total time was better than activity wheel turns which showed considerable variability among individuals and was therefore of little value. It appears that in using this method of evaluating the reliability of criteria for determining habitat preferences, Harris presupposes that the criterion which most strongly supports a definite habitat preference is the most reliable. One should consider the hypothetical situation of a mouse not actually preferring either of two habitats. One measure indicates a statistically significant preference while another does not. In this hypothetical situation, the measure indicating a preference would be the less reliable of the two, since we have said that the mouse has no preference. Perhaps for some reason, the one measure consistently shows a preference that does not actually exist. From this we can see that merely because one criterion is more often found to be statistically significant does not in itself make that criterion more reliable than others.

Table I reveals that Microtus pennsylvanicus demonstrated significant (the 95 percent level of significance is used for all statistical analyses in this paper) preference for the wet habitat according to the criteria of total time spent in a habitat, food consumed in a habitat and the percent of activity wheel revolutions

in a habitat. The actual number of activity wheel revolutions shows a preference for the wet habitat at slightly less than the 95 percent level of significance. Water consumption at night also shows preference for the wet habitat at a lower level of significance. Water consumption for the entire trial was nearly the same in each habitat. Since all four criteria indicate more utilization of the wet habitat, it appears that M. pennsylvanicus preferred a wet substrate to a dry one in this experiment.

The results obtained for Microtus montanus are somewhat harder to evaluate. Time spent in each habitat indicates that neither habitat was selected over the other. The number of activity wheel revolutions shows a slight preference for the wet habitat, but this preference is not statistically significant. Since results from this criterion are not statistically significant and the activity wheel method is probably the least reliable for determining habitat preferences, the activity wheel results will not be dealt with further. According to the food consumption data, a statistically significant preference is shown for the wet habitat. Water consumption, on the other hand, shows a statistically significant preference for the dry habitat. By looking at only one of the three more reliable criteria, three different conclusions could be drawn about the habitat preferences of M. montanus. But since the results of all three criteria must be considered, an attempt must be made to integrate the data into a probable, or at least possible, hypothesis.

If it is accepted that total time spent in each habitat is probably the most reliable method of determining habitat selection,

then we can say M. montanus did not make a choice between the two habitats. There does not seem to be any sure way of determining which of the two, water or food consumption, is the most reliable measure of habitat preferences. It is also not readily apparent why these two measures should yield results that point to completely opposite conclusions. Therefore it might be best to regard these measures as "canceling" each other and conclude that the results of this experiment do not indicate that M. montanus prefers either the dry or wet habitat.

In this type of experiment, more validity is associated with a positive result, a significant habitat preference, than a negative result, no significant habitat preference. This is especially true because the effect of uncontrolled factors in this experiment might be expected to randomize the voles activity and thus obscure a habitat preference if one existed. So the conclusion that Microtus pennsylvanicus shows a preference for wet substrate is probably more valid than the tentative conclusion that M. montanus does not show a preference for either substrate. This latter conclusion is made even less certain by the conflicting results obtained.

The data obtained from the habitat selection experiment are presented in the second, third, and fourth columns of Table I, which gives the mean values for the various measures. Examination of these data leads to the same conclusions obtained from the statistical analysis but, in addition, some interspecific comparisons of interest can be made.

Total food measures were more for Microtus pennsylvanicus than for M. montanus. Although the values are for food removed from the

dishes rather than actual food consumption, there may be a correlation between the two. In some trials, several grams of food were removed from the food dishes and either cached or left scattered around the habitat. However, in most cases, there was no evidence that food was removed from the dishes but not eaten. During the course of the experiment, individual instances of food caching were not recorded so it is not known whether one species did more food caching than the other. An indication of when food caching occurred can be derived by counting those trials in which more than 6, 8, or 10 grams of food were removed from the dishes. In using this method, one must assume that the vole does not normally eat more than 6 or 8 grams in a 24-hour period. During the experiment, food caching did occur in several trials in which 5 to 10 grams of food were removed so perhaps this assumption has some validity. Microtus montanus removed more than 6 grams of food from the dishes in 11 of 51 trials; more than 8 grams in 6 of 51 trials; more than 10 grams in 3 of 51 trials. Microtus pennsylvanicus removed more than 6 grams of food from the dishes in 17 of 39 trials; more than 8 grams in 9 of 39 trials; more than 10 grams in 6 of 39 trials. This indicates that M. pennsylvanicus may have done more food caching than M. montanus and this could partly account for the difference in mean amounts of food removed from the food dishes.

There is a difference also in the measures of water. These values are measures of actual consumption so it appears that M. pennsylvanicus drinks more water than M. montanus. This difference in water consumption will be discussed later.

Comparison of the mean number of activity wheel turns indicates that M. montanus were more active than M. pennsylvanicus. Microtus montanus also demonstrated digging activity in more trials than did M. pennsylvanicus; 21 of 51 trials versus 5 of 39 trials. Digging by Microtus montanus was also more extensive. This difference in digging activity is not unexpected as M. montanus inhabits dry areas of compact soil suitable for burrowing while M. pennsylvanicus lives in areas of wet soil which are not suitable for burrowing. No ready explanation of the differences in general activity as shown by number of activity wheel turns is discernible.

There is another interesting aspect of the digging and burrowing activity of M. montanus. Although some digging occurred in the dry substrate, most of the digging and all of the burrow-making took place in the wet soil. The dry soil in the habitat was crumbly rather than compact and therefore unsuitable for making burrows. Perhaps the compactness of the wet soil, which made it suitable for burrowing, induced M. montanus to spend more time in the wet habitat than it would have if the dry soil had been just as suitable for burrowing. If such a phenomenon occurred, it could have been a major factor in obscuring a possible preference for the dry habitat.

In the course of field studies on the prairie vole (Microtus ochrogaster), an approximate ecological equivalent of M. montanus that occurs in the Midwestern region of the United States, Jameson (1947) found that underground tunnels were most often constructed by the voles immediately after a heavy rain when the soil was moist. Such a tendency in M. montanus would help explain their use of the moist soil

in the artificial habitat.

Possible Factors Affecting Outcome of Habitat Selection Trials.

There were a number of uncontrolled factors which may have had an influence on the habitat choice of the voles. The presence of other caged animals in the experimental room and activities of people associated with them may have induced the voles to spend more time on the side farthest from the activity. The enclosure was covered with black rolled plastic material to reduce the effect of human activity in the room but this was probably not completely effective. At night there was less disturbance in the room, at least by people, than during the day. Lights were off, blinds covered the windows and, except for an occasional person passing through the far corner of the room to get to an adjacent room, people did not enter the room. Maintaining the enclosure in darkness during the day may have in some way affected the choice of habitat made by the voles, but I felt it was more important to try to isolate the habitat from the rest of the room than to maintain natural light conditions during the day.

Removing the cover in the evening to make measurements of food, water, and activity wheel revolutions, may have affected the vole's later activity. Occasionally causing the vole to cross through the passageway, no matter how subtly done and despite the fact that the vole experienced approximately the same amount of disturbance in each habitat, could only increase the likelihood of the vole's subsequent choice being affected. In about half of the trials, it was necessary for me to get into the dry habitat and repair the treadle system. The vole was not purposely disturbed on these occasions but my presence

was undoubtedly a disturbing factor. There is a strong possibility that individual voles may have reacted quite differently to the same degree of disturbance. It seemed that some of the bolder voles were scarcely bothered by my presence in the habitat while the more timid voles acted as though terrified.

Since the enclosure was covered almost 24 hours a day, evaporation from the wet soil caused conditions of unnaturally high humidity within the enclosure. Despite the free interchange of air between the two compartments, the humidity was probably higher in the wet habitat than it was in the dry. Whether this difference, if it existed, was great enough to influence a vole's choice of habitat is not known.

No effort was made to remove mouse droppings from the habitats, though occasional turning and mixing of the soil to keep it from becoming too compacted, particularly in the wet habitat, did reduce accumulation of droppings on the substrate surface. It is possible that metabolic wastes of the other species may have caused a vole to avoid one compartment or the other. Another possibility is that metabolic wastes of the same species may have had an attractive or repellent influence on a vole. In most cases, however, voles spent enough time in both compartments to make it seem likely that urination and defecation took place in both of them. There did not appear to be any constant influence on the habitat choice of a vole by the choice made by the vole in the immediately preceding trial.

The order in which the voles were used in the trials was an arbitrary decision on my part. Usually several of one species were

used, then several of the other species, et cetera. Neither species seemed to have other than random influence on the habitat choice made by the vole in the next trial.

It seems entirely possible that a vole might tend to make more use of the water dispenser, and possibly the food dish and activity wheel, which it used initially. No information was available or could be readily gathered which would confirm or reject this theory. Harris (1952) found that many of his Peromyscus maniculatus tended to return to the nest box first occupied in a test, and something of a similar nature might have occurred with the voles.

It is mentioned above that activity in the room containing the artificial habitats may have caused the voles to spend more time in the habitat furthest from the activity. One way to determine if this did occur is to analyze the results of trials in which an individual vole preferred the same compartment in each of two trials, regardless of the substrate (see Table II). The first column in Table II shows the number of voles, for each habitat preference measure, that showed a preference for the compartment nearest the source of activity in the room when the wet soil was there and again when dry soil was there. The second column shows the same information for the compartment furthest from the source of activity in the room. According to all the measures but food, there was more of a tendency for the voles to show a preference for the compartment away from the activity in the room than the one near the activity. The differences are not great, however, for the measures of time and food. So perhaps the effect of disturbances in the room on the voles was not too great and these

TABLE II

Summary of vole preferences for those individuals used in at least one trial both before and after the dry and wet substrates were interchanged.

	<u>Col. 1</u>	<u>Col. 2</u>	<u>Col. 3</u>	<u>Col. 4</u>	<u>Col. 5</u>	<u>Col. 6</u>
Measure	No. voles preferring compartment near activity	No. voles preferring compartment away from activity	No. voles preferring wet each trial	No. voles preferring dry each trial	Column 1 * Column 2	Column 3 * Column 4
Time	4	7	8	7	11	15
Food	7	6	14	2	13	16
Water	5	9	3	8	14	11
Activity wheel revolutions	5	9	8	7	14	15

voles may not have shown a definite habitat preference for some other reason.

Looking at Columns 5 and 6 of Table II, one can see that, of the voles used in at least one trial both before and after the dry and wet substrates were interchanged, almost half showed different habitat preferences according to time, food and activity wheel measures and more than half according to water consumption. So it appears that many voles did not have a constant preference, or, if they did, it was obscured by the effect of other factors.

Vole Interaction Experiment

One hundred and forty-five different combinations of voles were used in this experiment, all combinations of species and sex being represented (see Table III for number of trials of each combination). For each trial, the number of approaches and the nature of behavior at each approach was recorded. Arbitrary scales of behavior with values from 1 to 5 were set up for both the approaching and approached vole (see Table IV). Low values (1 and 2) correspond to submissive or avoidance behavior and high values (4 and 5) correspond to aggressive or agonistic behavior. A score of 3 indicates a neither submissive or agonistic type behavior referred to henceforth as fraternal. Values from these scales were assigned to both voles for each approach. To determine the total type of behavior for both voles at an approach, the following procedure was used. First, the numerical difference between 3 (neutral behavior) and the rank of behavior from Table IV assigned to a vole is determined for each vole involved in the approach. These two

TABLE III

Combinations of species and sex used in the behavior trials.

Combination	Number of Trials
<u>M. pennsylvanicus</u> male and <u>M. pennsylvanicus</u> male	13
<u>M. montanus</u> male and <u>M. montanus</u> male	13
<u>M. pennsylvanicus</u> male and <u>M. montanus</u> male	34
<u>M. pennsylvanicus</u> female and <u>M. pennsylvanicus</u> female	10
<u>M. montanus</u> female and <u>M. montanus</u> female	10
<u>M. pennsylvanicus</u> female and <u>M. montanus</u> female	25
<u>M. pennsylvanicus</u> male and <u>M. pennsylvanicus</u> female	10
<u>M. pennsylvanicus</u> male and <u>M. montanus</u> female	10
<u>M. montanus</u> male and <u>M. pennsylvanicus</u> female	10
<u>M. montanus</u> male and <u>M. montanus</u> female	10
Total	145

TABLE IV

Scales of behavior for approaching and approached voles.

Approaching vole	Approached vole
1. Vole retreats immediately.	1. Vole retreats immediately.
2. Vole sniffs a little towards other vole and then leaves or vole ignores other vole. No body contact.	2. Vole cowers or shows other signs of submissive behavior.
3. Vole sniffs at other vole or sits with it. Body contact occurs.	3. Vole sniffs back at other vole or sits with it. Body contact occurs.
4. Vole crawls on other vole; slight squeaking or other mildly agonistic behavior.	4. Vole squeaks, stands or exhibits other weak defensive activity.
5. Vole fights, spars vigorously, or bites.	5. Vole fights, spars vigorously, lunges or bites.

absolute numbers are then added together: $|A-3| + |B-3| = C$, where A equals ranking of one vole, B equals ranking of the second vole, and C is the sum of the two absolute numbers. The sum is declared positive if at least one of the rankings from Table IV is above 3. The sum is declared negative if one of the rankings from Table IV is less than or is 3, and the other is less than 3. If both rankings from Table IV are 3, the sum is 0. For example, if the rankings are both 4, the two absolute numbers (difference between ranking number and 3) are 1. The sum of the two absolute numbers is 2 and it is positive since at least one of the rankings is above 3. If the rankings are 2 and 4, the absolute numbers are each 1, their sum is 2, and it is positive as one of the rankings is above 3. If the rankings are 3 and 1, the absolute numbers are 0 and 2, their sum is 2, and it is negative since neither ranking is above 3. All possible combinations of rankings and the resultant absolute numbers and sums are presented in Table V. It is apparent from Table V that several different combinations of behavior rankings can result in the same C value (example: 5 and 4, 5 and 2, and 4 and 1 have the same C value of +3). A single C value may not denote exactly the same kind and intensity of behavior in each case. However, the general meaning of a single C value is the same no matter what combination of behavior rankings was involved in the calculation of it.

Values of C from -4 to +4 inclusive are possible. Positive values of C reflect varying degrees of agonism, the lowest intensity being 1 and the highest, 4. Negative values of C reflect varying degrees of submissive or avoidance behavior, the lowest intensity again

TABLE V

The results of all combinations of rankings from Table IV when inserted in the formula $|A-3| + |B-3| = C$ where A = ranking of one vole, B = ranking of other vole, and C is the sum of the two absolute numbers.

Rankings of the two voles		Absolute numbers		Sums of $ A-3 + B-3 $ (C)	Sign
A	B	$ A-3 $	$ B-3 $		
5	5	2	2	4	plus
5	1	2	2	4	plus
5	4	2	1	3	plus
5	2	2	1	3	plus
4	1	1	2	3	plus
5	3	2	0	2	plus
4	4	1	1	2	plus
4	2	1	1	2	plus
4	3	1	0	1	plus
3	3	0	0	0	zero
3	2	0	1	1	minus
2	2	1	1	2	minus
3	1	0	2	2	minus
2	1	1	2	3	minus
1	1	2	2	4	minus

being 1, the highest, 4. A value of 0 is indicative of fraternal behavior. For each combination of sex and species, the number of approaches for each C value of behavior were tabulated and frequencies of positive, negative, and zero C values for intraspecific and interspecific combinations were compared (Table VI). The Chi-square test for homogeneity (Dixon and Massey, 1957, Chapter 13) was used in making these comparisons.

In only four of the ten comparisons is there a difference of statistical significance (95 percent level or higher) between interspecific and intraspecific behavior. For example, in the comparison between the interspecific male combination and the intraspecific male M. pennsylvanicus combination we can see that the actual values for all three categories of behavior vary notably from the expected values. If the behavior in these two combinations was much alike, the actual values would more nearly coincide with the expected values. In this comparison it is apparent that for the interspecific trials, actual numbers of occurrences of agonism are lower than the expected frequency and actual frequencies of fraternalism and avoidance are more than the expected frequencies. The converse is true in the intraspecific trials.

Three of the comparisons with statistical significance involve interspecific combinations and intraspecific combinations of Microtus pennsylvanicus. More intraspecific agonism and less intraspecific fraternalism is shown in all three cases. The M. pennsylvanicus male-M. montanus female versus M. pennsylvanicus male-female combinations show more intraspecific avoidance while the other two comparisons reveal more interspecific avoidance. The only statistically significant

TABLE VI

Comparison of inter- and intraspecific behavior by the Chi-square test for homogeneity.

E = expected values A = actual values m = M. montanus p = M. pennsylvanicus

Values of C	Male p x Male m		Male p x Male p		Female p x Female m		Female p x Female p	
	A	E	A	E	A	E	A	E
Above 0 (agonism)	59	(73.2)	41	(26.8)	33	(35.2)	15	(12.8)
0 (fraternalism)	48	(39.5)	6	(14.5)	51	(49.9)	17	(18.1)
Below 0 (avoidance)	32	(26.4)	4	(9.6)	7	(5.9)	1	(2.1)
Significance	$\chi^2 = 21.54$ 99% confidence level				$\chi^2 = 1.387$ no significance			

Values of C	Male p x Female m		Male p x Female p		Female p x Male m		Female p x Male p	
	A	E	A	E	A	E	A	E
Above 0 (agonism)	17	(19.0)	21	(19.0)	12	(16.3)	21	(16.7)
0 (fraternalism)	18	(13.5)	9	(13.5)	12	(10.4)	9	(10.6)
Below 0 (avoidance)	0	(2.5)	5	(2.5)	10	(7.4)	5	(7.6)
Significance	$\chi^2 = 8.42$ 95% confidence level				$\chi^2 = 4.53$ no significance			

TABLE VI(continued)

Values of C	Male p x Male m		Male m x Male m		Female p x Female m		Female m x Female m	
	A	E	A	E	A	E	A	E
Above 0 (agonism)	59	(59.0)	22	(22.0)	33	(33.2)	17	(16.8)
0 (fraternalism)	48	(48.8)	19	(18.2)	51	(50.5)	25	(25.5)
Below 0 (avoidance)	32	(31.3)	11	(11.7)	7	(7.3)	4	(3.7)

Significance $\chi^2 = .105$ no significance $\chi^2 = .052$ no significance

Values of C	Male p x Female m		Male m x Female m		Male m x Female p		Male m x Female m	
	A	E	A	E	A	E	A	E
Above 0 (agonism)	17	(15.7)	18	(19.3)	12	(13.3)	18	(16.7)
0 (fraternalism)	18	(14.8)	15	(18.2)	12	(11.9)	15	(15.1)
Below 0 (avoidance)	0	(4.5)	10	(5.5)	10	(8.8)	10	(11.2)

Significance $\chi^2 = 9.51$ 95% confidence level $\chi^2 = .524$ no significance

TABLE VI (continued)

Values of C	m x p, both sexes		p x p, both sexes		m x p, both sexes		m x m, both sexes	
	A	E	A	E	A	E	A	E
Above 0 (agonism)	121	(134.0)	77	(64.0)	121	(113.6)	57	(64.4)
0 (fraternalism)	79	(75.1)	32	(35.9)	79	(88.0)	59	(50.0)
Below 0 (avoidance)	49	(39.9)	10	(19.1)	49	(47.4)	25	(26.6)
Significance	$\chi^2 = 10.92$ 99% confidence level				$\chi^2 = 4.022$ no significance			

difference involving an intraspecific combination of M. montanus is in the M. pennsylvanicus male-M. montanus female versus M. montanus male-female comparison where more interspecific fraternalism and more intraspecific avoidance occurs. The general picture presented by these comparisons may be seen best by referring to comparisons of all the intra- and interspecific combinations lumped together regardless of sex (see third page of Table VI). Whereas M. montanus intraspecific behavior is not significantly different from interspecific behavior in a statistical sense, there is significantly greater agonism, less fraternalism and less avoidance between M. pennsylvanicus individuals than between M. pennsylvanicus and M. montanus.

This method of treating the data does not allow a distinction to be made between mild and strong agonistic behavior or mild and strong avoidance behavior. By multiplying the numerical value (C) assigned to a type and intensity of behavior by the number of occurrences of that behavior, then summing the positive values and negative values separately, we incorporate the intensity of a particular type of behavior into the data. This type of data does not lend itself to statistical analysis but subjective comparisons can be made. The weighted values, above and below zero, and the number of occurrences of zero values, are divided by the total number of approaches involved in a given combination so direct comparisons can be made (see Table VII). This treatment of the data lends emphasis to the intensity of agonism and avoidance rather than just comparing the frequency of agonism and avoidance.

TABLE VII

Weighted values for agonism and avoidance for all combinations of species and sex. p = M. pennsylvanicus; m = M. montanus. See text (p. 42) for further explanation.

Combination	Above zero (agonism)	Zero (fraternalism)	Below zero (avoidance)
p x m, both sexes	.99	.36	-.21
p x p, both sexes	1.16	.27	-.14
m x m, both sexes	1.00	.42	-.33
Male p x Male m	1.24	.20	-.29
Male p x Male p	1.63	.12	-.16
Male m x Male m	1.02	.37	-.38
Female p x Female m	.63	.56	-.13
Female p x Female p	.76	.52	-.06
Female m x Female m	1.04	.54	-.15
Male p x Female m	1.37	.51	0
Male p x Female p	.86	.26	-.20
Male m x Female m	.93	.35	-.44
Female p x male m	.59	.35	-.32

Comparison of the male combinations shows that Microtus pennsylvanicus exhibited more agonism, less fraternalism and less avoidance intraspecifically than interspecifically. Microtus montanus, on the other hand, displayed about the same amount of agonism, more fraternalism and more avoidance intraspecifically than interspecifically. Female M. montanus showed more agonism among themselves than with M. pennsylvanicus. Female M. pennsylvanicus also showed more intraspecific agonism but also exhibited less avoidance behavior than with M. montanus. The combinations of M. pennsylvanicus male and M. montanus female showed more agonism and fraternalism and less avoidance than either intraspecific male-female combination. The combination of M. montanus male and M. pennsylvanicus female showed less agonism than either intraspecific male-female combination, more avoidance than the M. pennsylvanicus male-female combination, and less avoidance than the M. montanus male-female combination. Although there were variations with different combinations of sex (discussed later), the general picture again may be seen by comparing all the data regardless of the sex of the voles involved (first 3 lines of Table VII). There is less interspecific agonism and more fraternalism and avoidance than between M. pennsylvanicus individuals. There is more fraternalism and avoidance between M. montanus individuals than there is interspecifically, but intraspecific M. montanus agonism is about the same as interspecific agonism.

Several tentative conclusions may be drawn from these comparisons. Interactions among Microtus pennsylvanicus involve more agonism and less fraternalism and avoidance than interactions among M. montanus.

Interspecific agonism, fraternalism, and avoidance lie somewhere between the extremes associated with intraspecific interactions, as though the behavioral tendencies of each species were damped when interspecific interactions occurred. The most significant differences are between interspecific and intraspecific M. pennsylvanicus agonism and avoidance, there being less interspecific agonism and more interspecific avoidance.

Data from the observation trials reveal several other differences in the behavior of these two species of Microtus that are not apparent in Table VII. The frequency of fighting, as shown by the number of trials in which both voles exhibited rank 5 agonism was less between M. pennsylvanicus individuals than in interspecific or intraspecific M. montanus combinations. This criterion shows that fighting occurred in 36 percent of intraspecific M. pennsylvanicus trials, 61 percent of intraspecific M. montanus trials, and 61 percent of interspecific trials. The relative infrequency of fighting among M. pennsylvanicus may have been due to their more frequent display of defensive behavior. When one M. pennsylvanicus approached another, the approached individual usually stood up and squeaked or chattered the teeth. This defensive display was often sufficient to prevent the approaching vole from coming into contact with it, thus reducing the likelihood of a fight. Microtus montanus, on the other hand, infrequently exhibited defensive behavior when approached and intraspecific approaches usually resulted in mutual sniffing and body contact. Once body contact occurred, fighting was more likely to take place.

The high frequency of fighting in the interspecific trials seemed to be the result of the relative lack of defensive behavior in M. montanus; when a meadow vole approached a montane vole body contact usually occurred, thus increasing the probability of fighting.

Squeaking, chattering and "gnashing of teeth" occurred most often in connection with defensive behavior, so the frequency of occurrence of these noises may be regarded as an index of defensiveness. Audible squeaking by M. pennsylvanicus occurred in 40 of the 112 trials involving that species and other noises were produced in 10 of 112 trials. Squeaking by M. montanus took place in 17 of 112 trials and other audible noises were produced in none of the 112 trials.

Occasionally during the course of a trial, the two voles would sit together for several minutes at a time without visible signs of strife. This behavior, termed contactual behavior by Scott (1956), is here referred to as huddling. Between M. montanus individuals, huddling occurred in 6 of 33 trials. Between M. pennsylvanicus individuals, huddling occurred in 2 of 33 trials, one-third as often as in M. montanus. Huddling occurred in 4 of 79 interspecific trials. In many cases in the intraspecific M. montanus trials, there were signs of a tendency for huddling; voles would sit together without visible strife for 10 to 60 seconds several times within the 10-minute observation period. This tendency is apparent from the relatively high value for fraternalism in Table VII for intraspecific M. montanus trials. This type of behavior in M. pennsylvanicus was rare. The absence of a strong huddling tendency in M. pennsylvanicus is no doubt correlated with their well-developed defensive behavior. Conversely,

huddling in M. montanus is probably associated with reduced defensive behavior.

Dominance Relationships. In order to determine any dominance relationships that might exist between these two species, it would be desirable to observe the pairs of voles over a longer period of time. Ten minutes is often not long enough for dominant-subordinate relationships to become apparent to the observer. Although this experiment was not specifically designed to determine whether one of the species is dominant, there are several clues which are helpful in determining if a dominance relationship exists.

There is a correlation between the rankings in Table V and dominance. Scores of 4 and 5 are indicative of dominant behavior while scores of 1 and 2 indicate subordination. A score of 3 may be regarded as neutral. When the number of occurrences of each rank for Microtus pennsylvanicus and M. montanus in interspecific trials are compared by the Chi-square test for homogeneity (see Table VIII), a statistically significant difference is apparent. Microtus pennsylvanicus exhibited rank 4 agonism more often and rank 2 and 1 avoidance less often than M. montanus. Rank 5 agonism occurred with about the same frequency in both voles. Since rank 5 agonism corresponds to sparring and fighting, it seems reasonable that whenever it occurred it should have occurred in both voles at the same time. There is a direct relationship between rank 4 agonism and rank 1 and 2 avoidance; when rank 4 behavior was exhibited by one vole, the other vole usually exhibited rank 1 or 2 behavior. If each interspecific combination is tested separately, the same results occur with statistical

TABLE VIII

Occurrences of behavior rankings from Table IV in interspecific trials compared by Chi-square test for homogeneity.

E = expected frequencies; A = actual frequencies.

Behavior Ranking	<u>M. pennsylvanicus</u>		<u>M. montanus</u>	
	A	E	A	E
5	51	(49.5)	48	(49.5)
4	63	(40.0)	17	(40.0)
3	160	(164.5)	169	(164.5)
2	22	(31.0)	40	(31.0)
1	3	(14.0)	25	(14.0)

Chi-square 49.46
Significant at 99% confidence level

significance at the 99 percent level in three of the four combinations.

Dominance relationships are also indicated by analysis of another portion of the data from the observations on vole behavior. In the interspecific trials, M. pennsylvanicus approached M. montanus 159 times and retreated 86 times while M. montanus retreated 73 times. Microtus montanus approached M. pennsylvanicus 139 times and retreated 118 times while M. pennsylvanicus retreated 21 times. When tested for homogeneity by the Chi-square method (see Table IX), this difference in the number of times the approached vole leaves is statistically significant at the 99 percent level. Results from the intraspecific trials show that the approaching vole most often leaves first. This occurred in 100 of 120 opportunities in M. pennsylvanicus, and 99 of 135 opportunities in M. montanus. Assuming that the dominant species will tend to stay and the subordinate species tends to leave, M. pennsylvanicus again appears dominant over M. montanus.

In 18 of the interspecific trials in which considerable agonistic behavior occurred, it was possible to determine that one vole was dominant over the other. Microtus pennsylvanicus was the dominant in 17 of these cases while M. montanus was dominant only once. Sex of the voles did not have a constant effect in these interspecific combinations. In each of these cases, M. pennsylvanicus was the heavier of the two voles, indicating that physical size might be the main factor associated with dominance. If that were true, the dominant individual in intraspecific trials should also be the larger vole. Of the 17 intraspecific trials in which dominance was apparent, the heavier vole was dominant in 11, the lighter in 6 of the trials. This

TABLE IX

Approaches and departures in interspecific trials compared by Chi-square test for homogeneity.

E = expected frequencies; A = actual frequencies.

	<u>M. pennsylvanicus</u> approaches		<u>M. montanus</u> approaches	
	A	E	A	E
Approaching vole leaves	86	(108.9)	118	(95.1)
Approached vole leaves	73	(50.2)	21	(43.8)

Chi-square = 32.55
Significant at 99% confidence level

seems to indicate that it was not weight alone that allowed M. pennsylvanicus to dominate M. montanus. Some psychological mechanism may have been involved. In actual fighting, weight and height are an advantage and the larger vole usually has the upper hand. The mean, maximum, and minimum weights of each species and each sex of the voles used in the behavior observation trials are presented in Table X. In general, M. pennsylvanicus individuals are larger than M. montanus, particularly the males.

TABLE X

Mean, maximum, and minimum weights in grams for the voles used in the behavior experiment.

Species and Sex	Mean Weight	Maximum	Minimum
<u>M. pennsylvanicus</u> male	46 g	57 g	35 g
<u>M. pennsylvanicus</u> female	36 g	47 g	30 g
<u>M. montanus</u> male	34 g	43 g	30 g
<u>M. montanus</u> female	34 g	48 g	26 g

Differences In Behavior Due To Sex. As previously mentioned, there were some differences in intraspecific agonism between the sexes. Further examination of the agonism ratings for the three intraspecific sex combinations for each species (see Table VII) reveals the nature of these differences.

Looking first at Microtus montanus combinations, we see that agonism was about the same between males and between females. Males

were less fraternal but exhibited more submissive behavior than females. Interactions between sexes were marked by less agonism than between either males or females and about the same amount of fraternal and submissive behavior as shown between males.

The differences between male and female M. pennsylvanicus were even greater. Males exhibited agonism and submissive behavior more and fraternalism less than the females. Values for all three of these types of behavior in interactions between the sexes lie between the values for males and those for females.

The sexes involved in interspecific trials also had a bearing on behavior. Much more agonism occurred between males than between females and more agonism was displayed in the M. pennsylvanicus male-M. montanus female trials than in the M. pennsylvanicus female-M. montanus male trials.

Some idea of dominance relationships between the sexes may be deduced in the same manner that species dominance was determined. Table XI presents the frequency of occurrence of each rank of behavior for the male-female combinations. Again, associating rankings of 5 and 4 with dominance and rankings of 2 and 1 with subordination, it is apparent that in M. pennsylvanicus, the males were slightly dominant and in M. montanus neither was decidedly dominant. In the interspecific trials, M. pennsylvanicus was dominant in both combinations of sex. Of the seven M. montanus male-female trials where dominance relationships could be ascertained, the male was dominant three times, the female four times. The M. pennsylvanicus male was dominant in both intraspecific male-female trials where dominance could be determined.

TABLE XI

Frequencies of rankings of behavior from Table IV for male-female vole combinations. p = M. pennsylvanicus; m = M. montanus

Behavior Ranking	Male p x Female m		Male m x Female p		Male p x Female p		Male m x Female m	
	Male	Female	Male	Female	Male	Female	Male	Female
	5	10	9	0	0	2	1	7
4	7	1	1	11	13	6	6	5
3	18	23	18	18	14	23	20	25
2	0	2	12	5	6	4	8	5
1	0	0	3	0	0	1	2	2
Total Approaches	35		34		35		43	

Microtus pennsylvanicus was dominant in all five of the interspecific male-female trials in which dominance was apparent.

Dominance by males in the intraspecific M. pennsylvanicus interactions might be due partially to the larger size of the males (see Table X). Mean weights of the M. montanus males and females used in the experiment are the same. This could help explain the lack of dominance by either sex in the M. montanus interactions.

The stage of estrus in the females may have had some effect on their behavior. Determination of the stage of estrus in females was beyond the scope of this study so no information was obtained on the effect of estrus or anestrus on female vole behavior.

Behavior Descriptions. Detailed description of vole behavior is outside the scope of this study, but enough impressions of vole behavior were gathered to make comparisons with more descriptive studies possible. Clarke (1956) conducted a study on aggressive behavior exhibited by Microtus agrestis which included detailed descriptions of several types of intraspecific behavior. Some of the actions he described which were also observable in this study are listed below.

1. The subordinate vole sometimes turned over on its back when another vole approached; no attack occurred under these conditions. (This action appears to be similar to the attack-inhibiting behavior of exposing the neck which Schenkel (1948) described in wolves.)
2. The dominant sometimes fidgeted or "marked time" (rapid movement of feet up and down).
3. Toilet and grooming took place frequently in nonaggressive situations and sometimes occurred during pauses in agonistic situations.

4. When approached, subordinate voles either squatted, lunged at the approacher to drive it off, or rarely, attacked the approacher.
5. Voles dug in sawdust (shavings in my study) during both aggressive and nonaggressive situations.

Clarke also reported several types of vole behavior not apparent in this study, notably, waltzing, a sort of rapid moving around with much movement of the feet, and pulling at parts of each others bodies.

Getz (1962), in an experimental study of aggressive behavior of Microtus pennsylvanicus and M. ochrogaster, the prairie vole, also described the behavior of these voles in some detail. His descriptions of approaches and interactions between two individuals are for the most part applicable to my observations, although behavior exhibited in my study seemed more variable than the vole behavior described by Getz.

One type of behavior that neither Clarke nor Getz described was wild leaping about the cage by both voles. This behavior seemed to be triggered by a sudden movement of one vole which startled the other, or a sudden confrontation of the two, apparently unexpected by both. As soon as one vole reacted by leaping about, the other appeared to be frightened and also leaped around the cage. After a few seconds, the leaping stopped and both voles, appearing frightened, remained motionless for 10 to 90 seconds. Then more usual behavior resumed. This behavior took place twice in interspecific trials with M. montanus doing the initial leaping, and once in a M. montanus intraspecific trial. Occurrences of this behavior were fairly common in a cage kept at my home containing two or three M. montanus. Wirtz and Pearson (1960) observed similar leaping around the cage by Peromyscus leucopus

when approached by Microtus pennsylvanicus and King (1957) recorded this type of behavior by Peromyscus maniculatus when in the same cage with Mus musculus.

In these studies, Peromyscus appeared to be dominated by Microtus or Mus and leaping about the cage was associated with subordination in the Peromyscus. The absence of this behavior in M. pennsylvanicus and its presence in M. montanus is another indication of dominance by the former and subordination in the latter.

When fighting occurred, its duration was limited to 5 seconds or less in most instances. Several times, however, fights took place which lasted up to 20 or 30 seconds. These occasions provided an opportunity for observing some of the actions involved in a vigorous prolonged fight. Most of the activity took place while the voles were erect on their hind legs facing each other. Sparring with the front feet and attempts to administer bites in the neck region were the principal methods of attack. Both voles seemed to be trying to stand as tall as possible and administer blows with the front feet, thus forcing the other vole down and backward. The taller vole had the advantage in this respect, and it would overwhelm the other vole every few seconds and force it down. The taller vole pressed the attack when the other was down but usually after rolling around for a second or two, both voles again stood up and continued sparring and biting. On one occasion, the shorter vole was able to force the taller one down once or twice by leaping slightly into the air and momentarily assuming a position over the other. Sometimes the larger vole pushed the other vole until it lost its balance and tumbled over backward. Fighting

continued until one of the voles either stopped fighting back and the other then seemingly lost interest in the fight, or one of the voles retreated without pursuit. Neither of the combatants appeared to be hurt or to suffer any ill effects from these fights.

Perhaps the most impressive aspect of vole behavior apparent in this study is the behavioral variability between individuals and of an individual. Different voles often act quite differently in seemingly comparable situations. Sometimes a vole appears to exhibit different behavior under the same conditions at different times. Bailey (1924) observed a high degree of individuality among Microtus pennsylvanicus and Foster (1959) observed great individual behavioral variability within each of two races of Peromyscus maniculatus. Other observers have also stressed behavioral variability in studies of mammalian behavior (Balph and Stokes, 1963). However, Balph and Stokes (1963), in their study of Citellus armatus, stressed the fact that the ground squirrel possesses a "hard core of stereotyped behavior." Their observations were of natural populations of ground squirrels and this could partly explain their conclusions. Perhaps small mammals under natural conditions normally react to various stimuli in a stereotyped manner. When these animals are placed in artificial situations they may tend to modify their actions and exhibit more variable behavior. In other words, some mammals might usually act in a stereotyped manner under natural conditions, but still could be capable of exhibiting more variable behavior under artificial conditions, thus obscuring any stereotypy present.

DISCUSSION

Habitat selection has long been considered an important aspect of animal distribution, particularly on the ecological level. Many animal species do not occur in all areas within their geographical range where the physical and biotic environment is suitable for their existence. According to Miller (1942), this can be because "... (habitat) selection may limit the occurrence of a species far short of limiting factors involved in nutrition, reproduction, and safety from predators."

When one is considering habitat selection in a particular animal species, there are two principal questions to be answered: first, what are the proximate factors by which individuals of the species make a selection; and second, what is the ultimate factor which causes the habitat to be of survival value. Lack (1949) illustrates the concept of proximate and ultimate factors in relation to habitat selection by reference to an invertebrate which is found in nature only in waters between certain temperature limits. This invertebrate will survive in water beyond these temperature limits in the laboratory. Thus, temperature is the proximate factor controlling habitat selection. The ultimate factor determining survival is something else, perhaps competition for food with another species. The response to temperature has been evolved because the animal is thereby brought into the habitat where it can survive. Habitat or niche segregation is a phenomenon of ultimate survival value for two or more ecologically similar species occurring in the same geographical area. Habitat and niche segregation

may result from proximate factors related to habitat selection, psychological intolerance, special adaptations, or some other phenomenon.

Students of small mammal ecology have made numerous studies of habitat segregation to determine if it occurs, and if so, what factors are responsible. In many cases, habitat selection is one of the principle mechanisms involved in the maintenance of habitat segregation. Proximal factors involved in habitat selection can be classified as physical (climate, soil, etc.) or biotic (vegetation and other animals).

Pruitt (1953) emphasized the importance of explaining habitat selection on the basis of physical aspects of the environment if at all possible. He found that extreme heat and dryness in the summer and winter freezing of the soil prevented shorttail shrews (Blarina brevicauda) from occupying certain areas within its geographic range in Michigan. The physical character of the soil may also have been important in the shrew's choice of habitat. Getz (1960a) mentioned relatively high humidity, as well as food and cover, as being important habitat requirements of the shrews Blarina brevicauda and Sorex cinereus. Blarina seems to avoid habitats containing standing water. Some microtine rodents and shrews may be restricted to wet habitats because of physiological water requirements (Odum, 1944; Getz, 1960 and 1962). Chew (1951) studied water exchanges of some small mammals (Blarina brevicauda, Peromyscus leucopus, and Microtus ochrogaster) and found that the water balance of each could be correlated with availability of water and amount of evaporation in their habitats. The water turnover rate of Blarina is adapted to wet, humid habitats

and that of Microtus is adapted to dry habitats with low humidity. The water turnover rate of Peromyscus is similar to that of Microtus but the latter has a lower water loss through evaporation, perhaps an adaptation to its drier habitat. Vegetational characteristics of the environment have been found to be important in habitat selection in several species including shrews (Getz, 1960), Peromyscus leucopus (Bendell, 1961), and Microtus pennsylvanicus (Eadie, 1953; Wirtz and Pearson, 1960). Vegetation may be important as food or cover in some cases, but the physical character of vegetation may sometimes be involved.

Sometimes habitat segregation cannot readily be explained on the basis of habitat selection involving physical or vegetational factors of the environment. Then it may be instructive to examine the distributions of closely related species. As Ota and Jameson (1961) point out, it seems realistic to consider other closely related forms as prominent features of the habitat which might be as important as, or even more important than, the character of soil or vegetation in influencing habitat choice. In a monograph on the montane vole, Microtus montanus, Anderson (1959) emphasizes the possibility that competition with closely related species with similar habits affects the distribution and occurrence of M. montanus. Anderson classifies the effect of other species on a similar species into three categories: direct competition; indirect competition; and behavioral responses that preclude the occurrence of direct competition.

When two closely related species with quite similar ecological niches first come into a situation of coexistence, presumably competition

occurs between them. According to Gause's competitive exclusion principle, an ecological niche cannot be simultaneously and completely occupied by stabilized populations of more than one species (Koplin, 1962). So eventually, if neither species is eliminated in the area of coexistence, competition is reduced or eliminated as the species become more restricted to their optimum habitats or ecological niches (Odum, 1959) and develop behavioral or other attributes which permit coexistence without competition. Many kinds of niche segregation are possible, but only habitat segregation will be dealt with here. If habitat selection is the mechanism evolved which obviates competition, we have a situation identical to the one described by Lack above, interspecific competition being the ultimate factor involved.

There is a possibility of confusing two different concepts when discussing habitat differences in two sympatric species. Many adaptational differences between two ecologically similar species are differences in efficiency of utilization of the habitat, enabling one species to force another out of a habitat through competition. These adaptations are not involved in maintaining complete habitat segregation unless one species is not physically able to exist in a part of another species' habitat or active competition between the species occurs. Habitat segregation is perpetuated in non-competitive situations then by other mechanisms, one of which is habitat selection.

Factors involved in habitat segregation have been studied in a number of animals. Restriction to optimum habitat in two ecologically similar sympatric species may be based on morphological, physiological, or behavioral adaptations. Several species of Peromyscus differ in

gross foot morphology, perhaps enough to play a role in keeping these mice in separate areas (McCabe and Blanchard, 1950). Differences in water balance between Microtus pennsylvanicus and M. ochrogaster might be involved in their habitat segregation (Getz, 1963). Kalabuchov (1939) states that differences in time of daily activity in two species of murid field mice (Apodemus) may account for their habitat differences, one being principally diurnal, the other nocturnal. Microtus pennsylvanicus and Clethrionomys gapperi exhibit a number of differences in behavior that can be associated with their habitat segregation (Clough, 1963). Dice (1922) concluded that water, temperature, and humidity were not important in habitat differences between Peromyscus maniculatus and P. leucopus, and postulated that behavioral factors might be involved.

In some cases, active habitat selection has been found to be important in habitat segregation of two species. Harris (1952) found that two races of Peromyscus maniculatus selected artificial habitats (grass in one case, trees in the other) on the basis of recognition of physical characteristics of the vegetation. Microtus pennsylvanicus also may choose between two artificial habitats on the basis of simulated vegetation (Wirtz and Pearson, 1960). Visual stimuli presented by the gross structure of the vegetation have been found to be involved in habitat selection in some birds (Svardson, 1949; Klopfer, 1963).

Barbehenn (1961) presents the idea that one species may be psychologically dominant over another so that the presence of the dominant inhibits the use of space by a subordinate species. An example is his discovery that the presence of Peromyscus reduced

utilization of bait stations by Microtus.

In many cases it is difficult to determine what component or components of the habitat are responsible for habitat segregation. Klopfer (1962) postulates that psychological factors may be influential in some of these situations.

The problem of how a habitat recognition or psychological mechanism is passed from generation to generation has been little studied. Wecker (1962) presents some evidence indicating that genetic assimilation of originally acquired characteristics (the Baldwin effect) may be involved in habitat selection in Peromyscus maniculatus bairdii. Learning seems to play a part in habitat selection in chipping sparrows (Klopfer, 1963).

Many of the intricacies of habitat segregation and selection are still poorly known. It is apparent that numerous factors can be involved in the occurrence and maintenance of habitat segregation and an explanation of this phenomenon for one species need not be at all applicable to another species. Anderson (1959) sums up the problem in this way:

"In a general way at least the influence of habitat on the occurrence of most species is obvious. The details of the interrelationships of organisms and environment are not obvious; they are, in fact, incredibly complex."

The results of this study do not fully explain the mechanism involved in the habitat segregation of Microtus montanus and M. pennsylvanicus but do provide additional material on which to base a plausible explanation of the phenomenon.

The habitat selection experiment revealed that M. pennsylvanicus

selects wet soil substrate in preference to a dry soil substrate. Microtus montanus did not select either the dry or wet substrate. We must keep in mind, however, that M. montanus might have a habitat preference based on some factor other than soil moisture or it may have a preference for wet or dry substrate that did not show up in this experiment.

The meadow vole might be expected to show a definite preference for mesic and hydric situations as it has previously been found to normally swim and dive (Bailey, 1924; Blair, 1939; Peterson, 1947; Murie, 1960) and its water balance is poorly fitted for existing in dry habitats (Getz, 1963). Even where dry-adapted species of Microtus are absent, M. pennsylvanicus occurs in higher densities in mesic habitat than in dryer areas (Getz, 1960b). Several authors (Soper, 1946; Rust, 1946; Hamilton, 1943) have noted that M. pennsylvanicus occupies numerous different habitats, including dry areas, where dry-adapted congeners are absent. Perhaps the occurrence of meadow voles in dry, less suitable areas results from excessive intraspecific competition due to high densities. Despite the occupancy of dry areas on occasion, it seems clear that mesic areas are optimum habitat for M. pennsylvanicus.

Microtus montanus, on the other hand, seems not to be restricted to the dry habitat in the absence of M. pennsylvanicus. In some areas in Arizona, New Mexico, and Colorado, the montane vole is most often found in mesic habitat (Findley and Jones, 1962) and Dalquest (1948) states that they occupy damp meadows and marshes in Washington. Hall (1946) and Findley and Negus (1953) also found that montane voles commonly occupied wet habitats in Nevada and Colorado in areas outside

the range of the meadow vole. In southern Idaho, M. montanus lives in "sloughs and marshes overgrown with cattails, rushes and sedges and when irrigation is practiced, in hayfields, ditch banks and pasture lands" (Davis, 1939). In areas of Colorado where both species occur, Warren (1942) states that M. montanus "seems to prefer drier ground than the Saguache vole (M. pennsylvanicus) and is found much on the grassy hill-sides; at the same time it is found in the meadows."

The sum of information available on habitats of these two microtines leads to the conclusion that their optimum habitats are nearly identical, the montane vole's habitat including more xeric areas, and the meadow vole's habitat including slightly more hydric areas. Intuitively, it also would seem that mesic habitats would be optimum for both these microtines since vegetation serving for food and cover is more lush in the wetter areas.

Where the ranges of these voles overlap, Microtus pennsylvanicus, according to Findley (1954), is forced to retreat to moist marshy areas near water. Presumably, M. montanus is more efficient in filling the "dry, grassland Microtus" niche. Of more importance is the exclusion of M. montanus from its optimum (in regard to the physical and vegetative factors) or nearly optimum habitat. Both species then have restricted ecological distributions where these ranges overlap, the difference being that the meadow vole is restricted to its optimum niche while the montane vole appears to be forced to inhabit a sub-optimal habitat (see Figure 4).

The habitat restrictions imposed on each of these species by the other's presence probably originated as a result of competition.

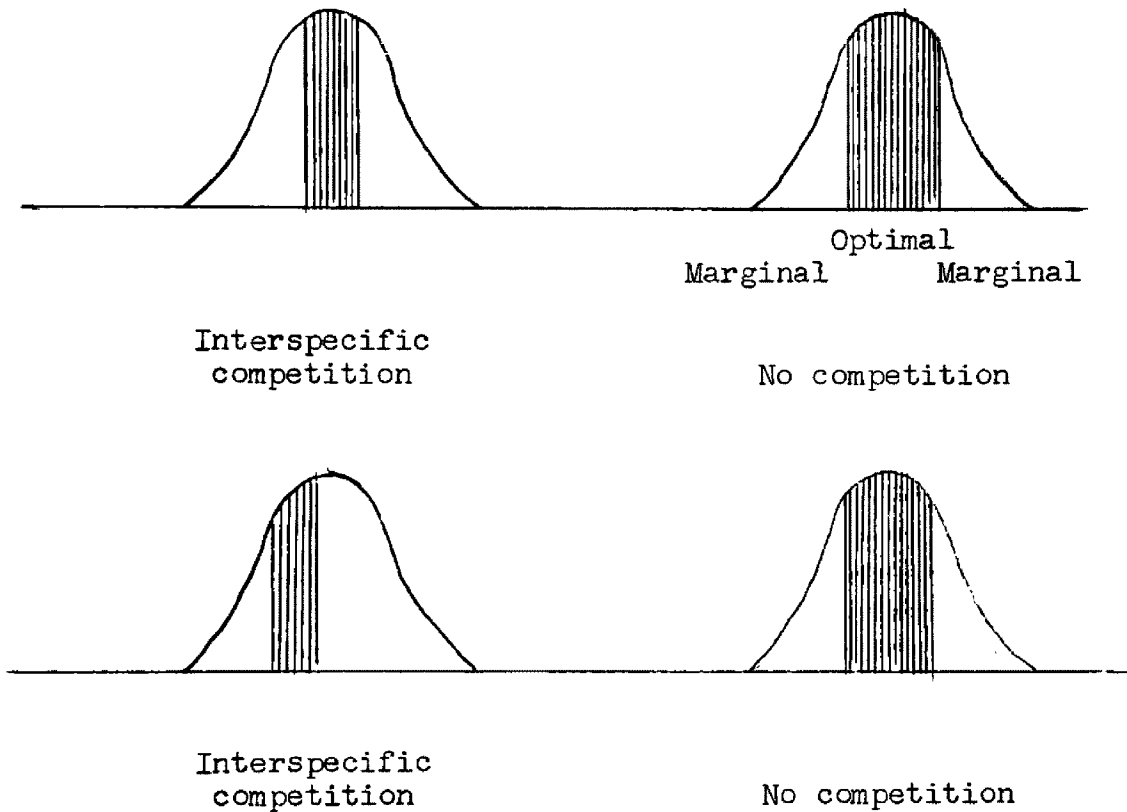


FIGURE 4

Effect of interspecific competition on habitat distribution
(modified from Odum, 1959).

Top: This is the situation occurring in M. pennsylvanicus--
restriction to optimum habitat in the presence of M.
montanus.

Bottom: This is the situation occurring in M. montanus--
restriction to sub-optimum habitat in the presence
of M. pennsylvanicus.

However, Koplín (1962) concluded that competition, defined by him as the "more or less excessive demand by two or more organisms for limited common niche factors, usually resources such as food and space", was not occurring between montane and meadow voles on the National Bison Range. Koplín suggested that habitat segregation is maintained by a mechanism of interspecific intolerance.

If interspecific intolerance does occur in these voles, one might assume that interspecific agonism would be greater than intraspecific agonism. Data from observations of the inter- and intraspecific interactions of these voles reveal that interspecific agonism is less than Microtus pennsylvanicus intraspecific agonism and about the same as M. montanus intraspecific agonism. Therefore the hypothesis that interspecific agonism is greater than intraspecific agonism must be rejected. Thus it appears that interspecific intolerance is not involved in maintaining habitat segregation. Before accepting this conclusion, however, it is worthwhile to examine the temperament and the nature of intraspecific interactions in the two species.

Microtus pennsylvanicus exhibited a great deal of intraspecific agonism and did a great deal of threatening by squeaking and sparring in the observational trials. Only rarely did members of this species cower or run from the other individual without first displaying some sort of agonistic behavior. When handled, they were quite prone to biting the hands and if chased around their cages a few times, they often would attack an approaching wire cone or gloved hand. On several occasions when two or more individuals were placed in the same cage while being transported from the field to the laboratory, one of

them was killed within 15 to 30 minutes. Other workers (Criddle, 1956; Getz, 1962) have also noted the aggressive nature of the meadow vole and Getz found that it was more aggressive intraspecifically than interspecifically with the prairie vole, Microtus ochrogaster. Getz (1961), in a field study of M. pennsylvanicus, also found indications that it may be territorial. Certainly meadow vole behavior in the laboratory is indicative of territoriality. If meadow voles are territorial, this goes hand in hand with their greater intraspecific agonism and high degree of defensive behavior mentioned earlier.

Microtus montanus has a temperament quite different from that of M. pennsylvanicus. The montane voles were not as combative; they fought very little and did not often display defensive squeaking or sparring. They also exhibited quite a lot of contactual or "huddling" behavior. When approached by another individual, M. montanus tended to run or cower rather than exhibit defensive behavior. All other aspects of their behavior also indicated a relatively docile and submissive nature.

All criteria used to determine dominance relationships between the species indicated that M. pennsylvanicus was dominant over M. montanus.

If we consider the foregoing information, it seems possible that the slight differences in behavior between interspecific and intraspecific interactions may be sufficient to keep the two species spatially separate in nature. This is indicated by dominant behavior of the meadow vole and the tendency for recessive or avoidance behavior in the montane vole. When the two species meet in nature without

the hindrance of cage walls, the slight differences apparent in the laboratory may be magnified, particularly the avoidance reaction of M. montanus and the defensiveness of M. pennsylvanicus. The meadow vole might not need to be as combative with montane voles due to the avoidance tendency in the latter.

Getz (1962) has conducted investigations of the intra- and interspecific behavior of Microtus pennsylvanicus and M. ochrogaster similar to the behavioral observations in this study. He found that M. ochrogaster was slightly dominant over M. pennsylvanicus despite the smaller size and more docile intraspecific behavior of the former. For this reason, Getz thought that where their ranges overlap, M. pennsylvanicus might be excluded from drier upland areas by the aggressive action of M. ochrogaster. This is directly opposite from my hypothesis that M. montanus is excluded from mesic areas by M. pennsylvanicus where their ranges overlap. Other than the dominance relationships with M. pennsylvanicus, montane and prairie voles have about the same temperament and perhaps similar habitat requirements and preferences. Getz did not feel that the dominance of M. ochrogaster over M. pennsylvanicus was sufficient to be the primary factor in their habitat differences in areas of sympatry. Rather, he thought other factors, such as a difference in water balance (Getz, 1963), were more important. The data on water consumption in my habitat selection trials indicate that M. montanus and M. pennsylvanicus may have a comparable difference in water balance, and this would account for differences in efficiency of utilizing dry habitat, perhaps being involved in original habitat segregation when the species became

sympatric. But since other studies have shown that both species survive in either wet or fairly dry habitat, a water balance difference would probably not in itself be functional in maintaining habitat segregation.

CONCLUSIONS

One objective of this study was to determine if the removal of Microtus pennsylvanicus from mesic habitat would induce M. montanus to move into the vacated area and establish centers of activity. No M. montanus were captured in the mesic area from which M. pennsylvanicus were removed but this was thought to be a result of the scarcity of M. montanus rather than any reluctance to enter the mesic habitat. No final conclusion to this problem can be drawn from the results obtained.

Data from the habitat selection trial reveal that M. pennsylvanicus exhibited a definite preference for the artificial habitat with a wet soil substrate. Microtus montanus did not exhibit a preference for either the wet or dry substrate. It is concluded that soil moisture probably does play a part in habitat selection of M. pennsylvanicus. Soil moisture probably is not in itself a major habitat selection factor in M. montanus though it must still be considered as possibly having some influence.

The hypothesis that interspecific agonism is greater than intraspecific agonism in M. montanus and M. pennsylvanicus must be rejected. However, the behavioral differences in these microtines indicate their habitat segregation may be maintained by a kind of intolerance mechanism without a great deal of agonism.

Habitat segregation in these two Microtus probably results from a difference in ability to utilize portions of their habitat. Under competitive conditions, M. pennsylvanicus apparently is better suited for living in mesic and hydric situations and M. montanus

appears to be more efficient in occupying the drier habitats. It is not known what makes one species better suited to one type of habitat and the other species better suited to another. Perhaps differences in water balance are important; or some other physiological or behavioral adaptations may be involved. This is a fertile area for further study.

The mechanism by which habitat segregation is maintained appears to have a different explanation. Microtus pennsylvanicus is dominant over M. montanus and in interactions between these two, the latter species demonstrates a strong escape tendency. This apparent psychological dominance, reinforced by actual physical dominance, may be sufficient to keep M. montanus out of mesic habitat occupied by M. pennsylvanicus.

Habitat preferences, as previously mentioned, may also play some part in the maintenance of habitat segregation of these species since M. pennsylvanicus does prefer wet soil under artificial conditions and might also respond positively to other features of the wet habitat. Perhaps M. montanus has also developed preferences for features of the dry habitat which could play a part in restricting it to those areas. Further experimental studies must be done before this matter is well understood.

SUMMARY

1. Investigation of habitat segregation in Microtus pennsylvanicus and M. montanus was commenced in July, 1962. Field work was done from July to October, 1962, and laboratory experiments were conducted from January through May, 1963. Objectives were threefold:

- (1) to determine if Microtus montanus would establish centers of activity in mesic habitat after reduction of M. pennsylvanicus;
- (2) to determine if soil moisture plays a part in the habitat segregation of these two species;
- (3) to determine if interspecific intolerance is involved in maintaining habitat segregation of the two species.

Field work was done on the National Bison Range, Moiese, Montana, and laboratory experiments were conducted in the Health Science Building on the Montana State University campus.

2. Live trapping on the National Bison Range from July to October, 1963, resulted in the removal of 39 M. pennsylvanicus from the mesic portion of the trap grid. No M. montanus were captured in the partially vacated mesic habitat. It was concluded that no M. montanus were caught because of their low population density rather than a reluctance to move into mesic habitat.

3. A two-compartment artificial habitat was constructed with wet soil in one side and dry soil in the other. A treadle system between the compartments was connected to a recorder, thus making it possible to determine the amount of time spent in each compartment.

Measures of food consumption, water consumption and activity wheel turns were also used in determining habitat preferences of the voles.

4. Ninety habitat selection trials of 24 hours duration were conducted, 51 with Microtus montanus and 39 with M. pennsylvanicus. Results of these trials led to the conclusions that M. pennsylvanicus showed a definite preference for the artificial habitat with a wet substrate but M. montanus did not demonstrate a preference for either dry or wet substrate.

5. The habitat selection trials indicated that M. pennsylvanicus drank more water than M. montanus and M. montanus was more active, particularly in regard to digging and burrowing, than M. pennsylvanicus.

6. One hundred and forty-five 10-minute observational trials of vole pairs were conducted. All combinations of species and sex were used. Analysis of data gathered from the observational trials revealed that interactions between Microtus pennsylvanicus individuals involved more agonism, less fraternalism, and less avoidance than interactions between M. montanus individuals. Interspecific interactions involved amounts of fraternal and avoidance behavior which lay between the values for the intraspecific trials. Agonism was slightly less than in intraspecific trials. Some sexual differences in behavior were apparent.

7. Microtus pennsylvanicus possessed well-developed defensive behavior which was nearly nonexistent in M. montanus. Microtus montanus exhibited "huddling" behavior quite often while M. pennsylvanicus only rarely exhibited this behavior.

8. Microtus pennsylvanicus were dominant over M. montanus. Within the former species, males seemed to dominate females; within the

latter species, no definite dominance relationship between the sexes was apparent.

9. A great deal of behavioral variability was apparent between individuals and in a single individual.

10. Some aspects of Microtus behavior were compared to descriptions of their behavior in other studies. Fighting and wild leaping behavior observed in this study were described.

11. Aspects of habitat selection and habitat segregation were discussed.

12. It was postulated that in areas of range overlap, M. pennsylvanicus is restricted to its optimum habitat and M. montanus is limited to a sub-optimal habitat.

13. The nature of differences in behavior and temperament between these two species indicate that habitat segregation may be maintained by interspecific intolerance without a great deal of agonistic interaction. Habitat selection may be of some importance in the maintenance of habitat segregation.

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