

HABITAT REQUIREMENTS AND HABITAT RESTRICTION OF MICROTUS
CHROTORRHINUS IN NORTHEASTERN MINNESOTA

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INTRODUCTION

Microtus chrotorrhinus, the rock vole or yellow-nosed vole, is among the most poorly known microtine rodents in North America. Throughout most of its range, including northeastern Minnesota, the rock vole typically has a very "patchy", discontinuous distribution. This pattern is likely a result of restriction to rather specialized, unevenly distributed habitats, but this problem is not well understood. Our knowledge about the specific habitat and microhabitat requirements of rock voles is at best incomplete. Qualitative descriptions of rock vole habitats in Minnesota and elsewhere have been provided by Buech et al. (1977), Daniels (1980, 1981), Kirkland (1977), Kirkland and Knipe (1979), Martell and Radvanyi (1977), Martin (1971), Timm et al. (1977), and others. Although these reports suggest some unifying, common characteristics of sites where rock voles occur (e.g., high moisture levels, thick moist litter), they also indicate considerable site-to-site variation. For example, the Minnesota localities for the species represent a variety of plant community types, shrub layer densities, and degrees of canopy closure. This same diversity among sites was apparent in surveys of Cook County, Minnesota in 1982, during which 53 new rock vole localities were discovered (Christian 1982). The direct significance of the presence of rocks, boulders, or talus, traditionally considered an essential feature of rock vole habitat, has been questioned (Buech et al. 1977); however, boulders were present at all new sites for the species found during 1982 (Christian 1982). Although rock voles have commonly been associated with undisturbed boreal or montane forests, recent evidence suggests that their distribution may include more characteristically-temperate-zone forests than previously thought, and that habitat disturbance may be important (Kirkland and Knipe 1979, Martell and

Radvanyi 1977). Thus, the vegetative and physical habitat features required by rock voles are unclear.

Associated with this problem, we lack information about M. chrotorrhinus' habitat breadth/degree of habitat specificity. Data on this problem are needed to understand the extent to which rock voles are isolated in very small habitat patches and thus occur in extremely small, local populations. For example, as noted above, all of the rock voles captured during the recent survey by Christian (1982) were found in close association with boulder deposits. A substantial number of these sites was represented by extremely small pockets of boulders or by only moderately sized boulder fields. It is unknown whether the habitat requirements of M. chrotorrhinus are specialized to the extent that only the rocky portions of these sites, and not adjacent, non-boulder areas, are suitable habitat. If this is the case, it would appear that many of the known Minnesota localities could support relatively few rock voles, and it is questionable whether such habitats could sustain viable populations from year to year. This suggestion is based on a reasonably well-supported ecological generalization -- derived from research on island populations -- that probabilities of local extinction are inversely related to island (in this case, habitat patch) size. Timm (1975), in a survey of Cook County small mammals during the early 1970's, sampled a large number of rock outcrops and boulder fields that were apparently reasonable-quality rock vole habitat but were of limited extent; he found the complete absence of rock voles at these sites. In contrast, as noted above, rock voles were frequently found in this type of habitat in 1982 (Christian 1982). The results of these studies provide circumstantial evidence that rock vole populations in such small-area habitats may, in fact, be unstable over periods of several years. Thus, habitat requirements and degree of habitat specialization may

be closely related to the long-term stability of rock vole populations in Minnesota.

Knowledge about these problems is needed to understand the status and biology of this species in the state and, if necessary, to formulate effective management strategies. The research described in this report was designed to examine these aspects of rock vole distribution in northeastern Minnesota. The general direction of the research involved examination of habitat and microhabitat requirements by comparing physical and vegetative features of rock vole capture sites with those where the species did not occur. The research also relied heavily on a comparative approach: it was felt that a useful means of understanding the habitat requirements of M. chrotorrhinus was to contrast this species' patterns with those of coexisting small rodents (see Christian 1980). Funding for this research was provided by the Minnesota Department of Natural Resources Nongame Program and by the University of Minnesota Graduate School; USDA Forest Service personnel are acknowledged for their cooperation. This work was conducted by the principal investigator, co-investigator Jeanne Daniels, and field assistants C. McDonough, P. Monson, and R. Smith.

STUDY AREAS

This research was conducted on three rock vole populations along the Gunflint Trail in T. 64N, R. 1E, Cook County, Minnesota. One of these sites is SE of Swamper Lake, 27 km N and 2 km W of Grand Marais. This is the site of the first recent record of rock voles in Minnesota, and has been described by Timm (1974, 1975) and Timm et al. (1977). The other two populations are among those discovered by Daniels (1980). One of these is located approximately 1 km SE of the above site and is SE of the intersection of the Gunflint Trail and Forest Service Road 316. The third site, located on Forest Service Road 152 about 1.9 km W of its intersection with the Gunflint Trail, is situated on the south bank of the North Brule River. These sites will hereafter be referred to respectively as the "Swamper", "316", and "Brule" sites. Because they are located in close proximity to one another, the three sites could be studied efficiently and more or less simultaneously.

All three sites are represented by open fields of exposed boulders surrounded by forest. The boulder field at the Swamper site is approximately 1.2 km long (Timm et al. 1977) and generally less than 60-90 m wide. Boulder fields at the other two sites are less extensive. That at the 316 site is oval-shaped and about 100 m long. The boulder field at the Brule site is about 140 m long and less than about 40 m wide; the north edge of this field is separated from the Brule River by only a narrow strip of land. Species composition of the adjacent forest was broadly similar at all three sites, with black spruce (Picea mariana), paper birch (Betula papyrifera), aspen (Populus tremuloides), and balsam fir (Abies balsamea) predominating. White cedar (Thuja occidentalis) was common at the Brule site but not at the other two. Other canopy species present at low density

at these sites included white pine (Pinus strobus), jack pine (Pinus banksiana), and tamarack (Larix laricina). Table 1 provides a list of the common herbaceous and shrub-layer vegetation found at the three sites. Species composition was roughly comparable at all three areas although, as described below, density (especially in the shrub layer) varied somewhat among the three. In general, "islands" of shrub vegetation were more abundant on the boulder field at the Swamper site than at the other two areas. Exposed boulders at all three sites were partially to largely covered with moss and lichens.

METHODS AND MATERIALS

Small rodent microhabitat distribution at each area was studied by mark-release-recapture live-trapping. Physical and vegetative characteristics of all trapping sites on each area were measured. Patterns of microhabitat use for each species of interest were assessed by comparing the qualities of trap sites where the species was captured with those where it was absent. The number of traps and the configuration of trap placement differed among areas. At the Swamper site, 135 trap stations were arranged in a grid of 15 parallel rows with 9 stations in each row. The middle trap station in each row was situated roughly in the center of the exposed boulder field; each row extended on both ends into the adjacent forest where boulders and crevices are generally absent. The interval between rows was 16m and between trap stations in a row was 8 m.

Fewer traps were used at the smaller areas. At these sites, traps were arranged to sample vegetatively and physically different portions of the site as efficiently as possible. At the 316 site, 63 trap stations were arranged in 3 rows circumscribing most of the perimeter of the boulder

Table 1. Common herbaceous and shrub-layer plants at three sites in Cook County, MN, where habitat and microhabitat requirements of M. chrotorrhinus were studied during 1982.

<u>Herbaceous Layer</u>	<u>Shrub Layer</u>
Bunchberry (<u>Cornus canadensis</u>)	Alder (<u>Alnus</u>)
Blueberry (<u>Vaccinium angustifolium</u>)	Hazel (<u>Corylus</u>)
Raspberry (<u>Rubus</u>)	Juneberry (<u>Amelanchier</u>)
Sarsaparilla (<u>Aralia nudicaulis</u>)	Willow (<u>Salix</u>)
Large-leafed Aster (<u>Aster macrophyllus</u>)	Mountain Maple (<u>Acer spicatum</u>)
Twinflower (<u>Linnaea borealis</u>)	Seedlings:
Bush Honeysuckle (<u>Diervilla lonicera</u>)	<u>Abies balsamea</u>
Lily-of-the-valley (<u>Maianthemum canadense</u>)	<u>Picea mariana</u>
Clinton's lily (<u>Clintonia borealis</u>)	
Rose (<u>Rosa acicularis</u>)	
Violet (<u>Viola</u>)	
Thimbleberry (<u>Rubus parviflorus</u>)	
Honeysuckle (<u>Lonicera</u> sp.)	
Starflower (<u>Trientalis borealis</u>)	
Wintergreen (<u>Gaultheria procumbens</u>)	
Strawberry (<u>Fragaria</u>)	
Labrador Tea (<u>Ledum groenlandicum</u>)	

field. One row followed the interface between open boulders and surrounding forest; previous work has shown this zone to be a preferred microhabitat of rock voles. The other two rows paralleled this one, with one situated 8m from the edge into the open boulders, the other 8m into the adjacent forest. The distance between traps in a row was 8m.

At the Brule site, 80 trap stations were placed in 4 parallel lines of 20 stations each running the full length of the exposed boulder field. Separate lines followed the approximate center, the north edge, and the south edge of the exposed boulder field. The fourth line was situated 8 m into the adjacent forest from the line on the south edge of the field. Because the perimeter of the field was somewhat irregular, the distance between the first 3 lines was variable. Within a line, the interval between trap stations was 8m.

One folding Sherman aluminum live trap (23 x 9 x 8 cm) was placed at each trap station. Traps were baited with a dry mixture of rolled oats and peanut butter. Trapping was conducted on each area for 4 nights and 3 days. On the Swamper area, traps were initially set on the afternoon of 23 August and were checked and removed on the morning of 27 August. On 24-26 August, traps were checked and re-baited in the early morning, around noon, and late afternoon/early evening. A similar schedule was used in trapping on the other areas, which were both sampled from 27 - 31 August.

Each Microtus chrotorrhinus, as well as Clethrionomys gapperi and Peromyscus maniculatus (the most common other species on all areas) was toe-clipped with a unique identification number for individual recognition. At first capture, the following data were recorded for individuals of these species: location on the trapping grid, body weight to the nearest g, sex, and reproductive condition. The latter included, for males, position of

testes (scrotal or abdominal); for females, condition of the vaginal opening (perforate or non-perforate), relative size of nipples (small, medium, or large; used as an indication of lactation), and signs of obvious pregnancy (i. e., bulging abdomen). At subsequent captures, only the animal's identification number and the trap station number of capture were noted. Other species (chipmunks, jumping mice, shrews) were not toe-clipped, and the only information recorded for these species was location on the trapping grid.

A variety of habitat parameters was assessed at each trapping station. These included several different expressions of vegetation density. Percentage ground cover was visually estimated (to the nearest 10%) by determining the coverage by herbs and grass/sedge inside a 50 x 25 cm wire frame. Percent canopy coverage (to the nearest 10%) was measured by viewing through an upright metal tube (11-cm diameter by 18-cm length) divided into quartiles by cross-hairs; the percent coverage of the observed circle by the canopy was visually estimated. An index of vegetative cover density (roughly, shrub-layer coverage) from 0-1m and from 1-2m above ground level was determined using a "cover density board" technique (DeVos and Mosby 1969). The density board was 2m tall and 9cm wide and was painted black and white in vertically alternating bands of 25cm height. Each band was painted with a large number (from 1 to 8 in order from bottom to top) in contrasting color. The board was held upright at a trapping station while an observer standing 6 m away recorded the numbers that were obstructed by vegetation; the count of these numbers in each of the two strata was directly related to density of vegetation. Three randomized measurements of ground cover, canopy coverage, and vegetative cover density were made at each trap station. The mean of the three values for each parameter was used to express density of vegetation at each site.

A tally of herbaceous, shrub/sapling, and canopy plant species at each trap site was made. The following coded variables were determined for each trap station: 1) standing or running water (present or absent); 2) soil development (none, medium, or good); 3) moss and lichen cover (none, medium, or thick); 4) exposed boulders (present or absent; if present, representative diameters were recorded); 5) crevices absent, few, or abundant; if present, typical depths were recorded); 6) leaf litter (none, scattered, or thick); and 7) fallen trees/logs (none, few, or abundant).

After trapping had been completed on the Swamper site, measurements of ambient humidity were made at selected M. chrotorrhinus capture sites and at control trap stations where the species was not caught. Readings were taken with a battery-operated psychrometer 0.5 m above the ground surface, within about 1 cm of the ground surface and, if crevices were present, at a depth of 15-20 cm below ground. Light penetration at the ground surface was measured at selected rock vole capture and non-capture sites using an Ozalid paper technique described by Friend (1961).

RESULTS

Trapping Results. Capture statistics for Microtus chrotorrhinus, Clethrionomys gapperi, and Peromyscus maniculatus at the Swamper site are shown in Table 2; capture data for the 316 and Brule sites are presented in Table 3. Other mammal species captured at the Swamper site included (number of captures in parentheses) Sorex cinereus (13), Blarina brevicauda (11), Eutamias minimus (10), Tamias striatus (7), Napeozapus insignis (2), and Zapus hudsonius (1). Captures of other mammals at the 316 site were E. minimus (18), B. brevicauda (13), S. cinereus (7), and Mustela erminea (1). At the Brule site, the only other mammals captured were B. brevicauda

(14 captures) and S. cinereus (8 captures). These other species will not be considered further.

Data presented in Table 2 indicate that rock voles, red-backed voles, and deer mice were caught in adequate numbers and at a sufficient number of trap stations at the Swamper site to analyze patterns of microhabitat use. Recapture rates were reasonably high for all three species. Data on the proportion of each day's catch represented by previously marked animals indicate that the trapping procedure was quite efficient for the two microtine rodents but only moderately so for deer mice. The distribution of captures among morning, noon, and afternoon trap-checks indicates that both vole species were reasonably active day and night, while a high proportion of P. maniculatus' activity was nocturnal. Population sizes were estimated as the minimum number of animals known alive by direct enumeration (Krebs 1966) and by two methods of mark-recapture analysis (Caughley 1977). As shown in Table 2, population size estimated by Schumacher's method agrees closely with the minimum number estimate for all three species. Estimates by Bailey's triple-catch method (computed using data from the first three days' trapping) are below the known minimum population sizes and thus are clearly underestimates. The minimum number estimates and Schumacher's estimates should be used as the most reasonable indicator of relative population sizes of the three species on the area.

The original objective of this research was to examine microhabitat distribution of M. chrotorrhinus at all three areas, thereby incorporating greater generality into conclusions about microhabitat requirements of the species. However, as shown in Table 3, rock voles were found only at low density on the 316 and Brule sites. At the 316 area, the total number of captures per trap-night for M. chrotorrhinus, C. gapperi, and P. maniculatus was identical to that on the Swamper grid (0.56/trap-night), but the

Table 2. Descriptive capture statistics and estimated population sizes for Microtus chrotorrhinus, Clethrionomys gapperi, and Peromyscus maniculatus at the Swamper boulder stream, Cook County, MN, during late August 1982.

CAPTURE STATISTICS	<u>M. chrotorrhinus</u>	<u>C. gapperi</u>	<u>P. maniculatus</u>
Number of individuals	20	59	21
Number of captures	57	192	48
Captures/trap-night	.11	.36	.09
Mean captures/animal	2.8	3.2	2.3
Number trap stations	34	89	36
Proportion recaptures			
Day 2	.55	.50	.43
Day 3	.82	.87	.55
Day 4	.86	.86	.69
Time of captures (proportion of total):			
AM	.48	.55	.72
Noon	.18	.12	.19
PM	.34	.33	.09
POPULATION SIZE ESTIMATES			
Minimum Number Known Alive	20	59	21
Schumacher's Method	22	60	22
Bailey's Triple Catch	18	49	6

Table 3. Descriptive capture statistics and estimated population sizes for M. chrotorrhinus, C. gapperi, and P. maniculatus at the 316 and Brule River boulder streams, Cook County, MN, during late August 1982.

316 Site

<u>CAPTURE STATISTICS</u>	<u>M. chrotorrhinus</u>	<u>C. gapperi</u>	<u>P. maniculatus</u>
Number of individuals	3	29	14
Number of captures	6	102	34
Captures/trap-night	.024	.405	.135
Number trap stations	6	36	21
<u>POPULATION SIZES</u>			
Minimum Number Known Alive	3	29	14
Schumacher's Method	-	29	16
Bailey's Triple Catch	-	12	37

Brule Site

<u>CAPTURE STATISTICS</u>			
Number of individuals	9	17	12
Number of captures	17	38	18
Captures/trap-night	.053	.119	.056
Number trap stations	10	24	17
<u>POPULATION SIZES</u>			
Minimum Number Known Alive	9	17	12
Schumacher's Method	12	19	16

captures/trap-night of rock voles was only about 1/5 that at the Swamper area. Only 3 rock voles were captured at a total of only 6 trap stations. At the Brule area, overall rodent density was low, as reflected by the fact that the total number of captures/trap-night for the three major species was only about 40% that on the other areas. While the abundance of M. chrotorrhinus at the Brule area was high relative to that of C. gapperi and P. maniculatus, data for only 9 rock voles captured at 10 trap stations are inadequate for quantitative examination of microhabitat distribution. Therefore, microhabitat preferences on the 316 and Brule sites were not analyzed and are discussed below only in general terms. Data from all three areas were used, however, to contrast the properties of high-quality rock vole habitat (the Swamper boulder stream) and of apparently less desirable habitat for the species (the 316 and Brule areas).

On the Swamper area, mean body weights of M. chrotorrhinus, C. gapperi, and P. maniculatus were, respectively, 23 g, 18 g, and 16 g. Only one relatively large (36 g) rock vole was captured; 3 of the 20 individuals were juveniles, and most appeared to be young-of-the-year subadults and young adults. Juvenile red-backed voles and deer mice were also present, suggesting low-level, on-going recruitment in all three species. Values for most breeding measures suggest that rock voles were slightly less active reproductively than the other two species. No M. chrotorrhinus males had testes in a scrotal position, while 0.2 and 0.18, respectively, of the male C. gapperi and P. maniculatus were in breeding condition. While proportions of females with perforate vaginas were similar in all three species (0.31-0.40), no lactating rock voles were captured, while a few females of the other two species had enlarged nipples. The only obviously pregnant animals captured were C. gapperi (3 of 39, or 0.08, females).

Microhabitat Distribution. The distribution of Swamper grid trap stations where M. chrotorrhinus, C. gapperi, and P. maniculatus were captured is shown in Figures 1, 2, and 3, respectively. These figures illustrate the approximate outline of the continuous field of exposed boulders and abundant crevices, which represented roughly 48% of the surface area covered by the live-trapping grid. It should be emphasized, as pointed out above, that numerous vegetation "islands" were present on the field. About 82% of the trap stations where M. chrotorrhinus were captured, and 93% of the total rock vole captures, were on the boulder field. Only 1 (3%) of the trap stations where this species was found represented the first or last trap station in a row. All traps where more than one M. chrotorrhinus capture was recorded were within the perimeter of the boulder field. In contrast, only 47% and 39%, respectively, of the trap stations where C. gapperi and P. maniculatus were captured, and 48% and 40% of the total captures of these species, were on the boulder field. Twenty-two percent and 28% of the trap stations where these two species were captured represented first and last stations in a row. Chi-square analyses on the data for trap-station-of-capture indicate that the distribution of M. chrotorrhinus in boulder-field trap stations and in end-of-row traps departs significantly from randomness ($P < 0.025$ in both cases). In contrast, these distributions for C. gapperi and P. maniculatus are not significantly different from a random pattern ($P > 0.50$ in all comparisons.) Furthermore, C. gapperi and P. maniculatus do not differ from each other in distribution in boulder field traps or in end-of line traps (both $P > 0.60$); distributions for both of these species differ from that of M. chrotorrhinus at respective probability levels of $P < 0.025$ and $P = 0.06-0.07$. These general differences in association with the boulder field

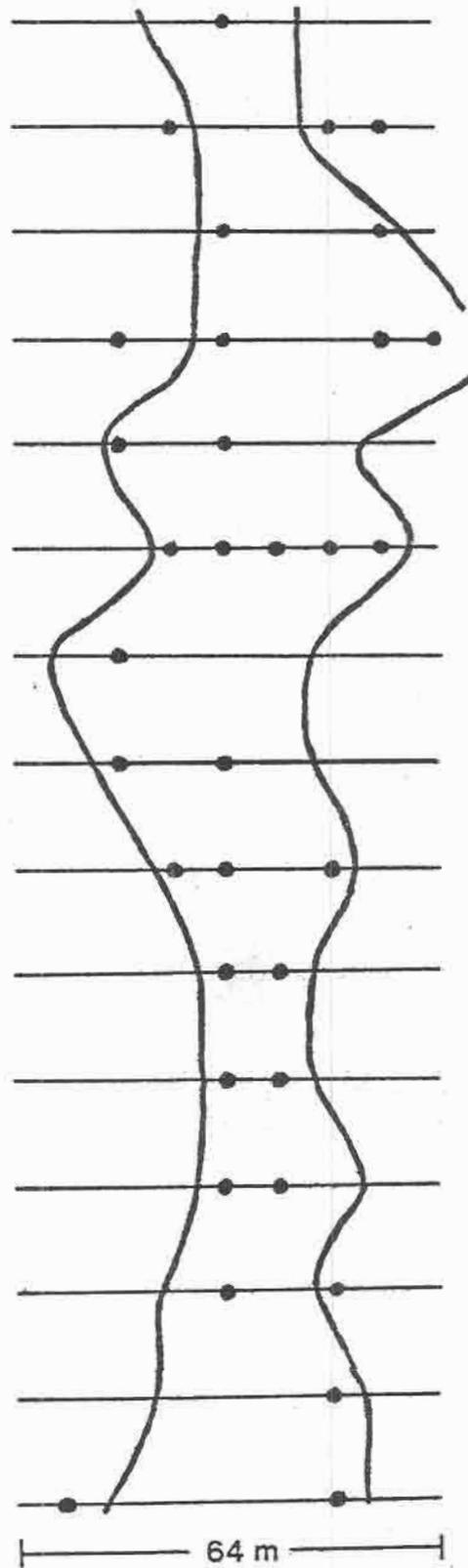


Figure 1. Distribution of capture stations for Microtus chrotorrhinus on the Swamper grid. Each horizontal line represents a row of 9 trap stations, with 8 m between traps in a row and 16 m between rows. The major axis of the grid has been linearized for ease of presentation.

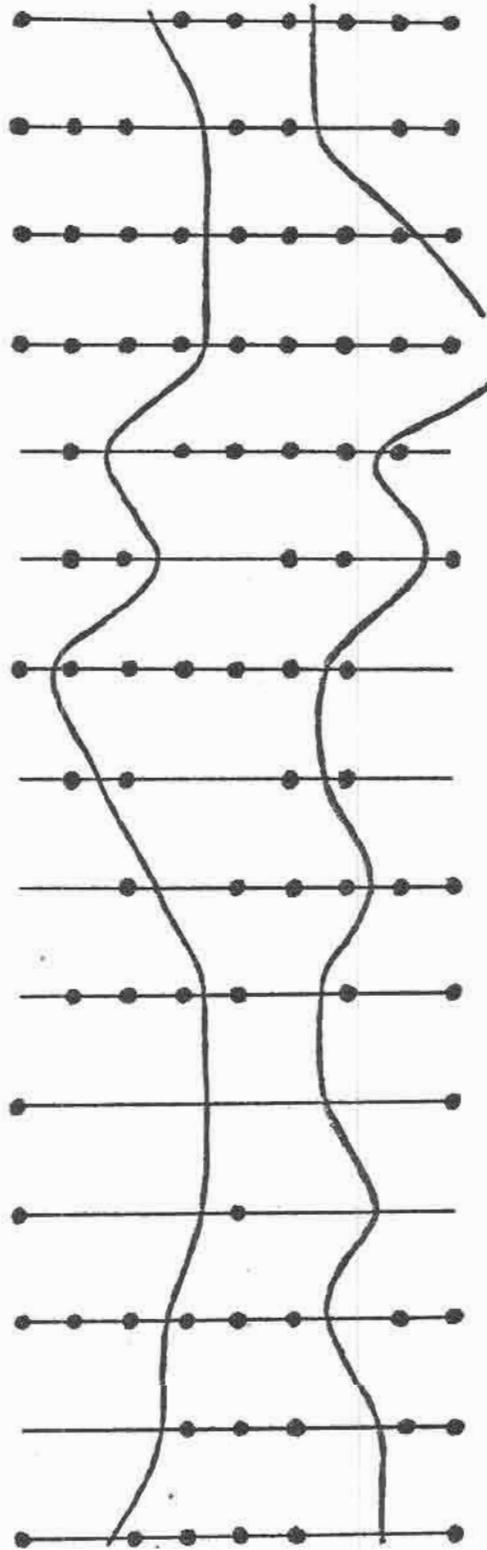


Figure 2. Distribution of capture stations for *Clethrionomys gapperi* on the Swamper grid. See Figure 1 for further information.

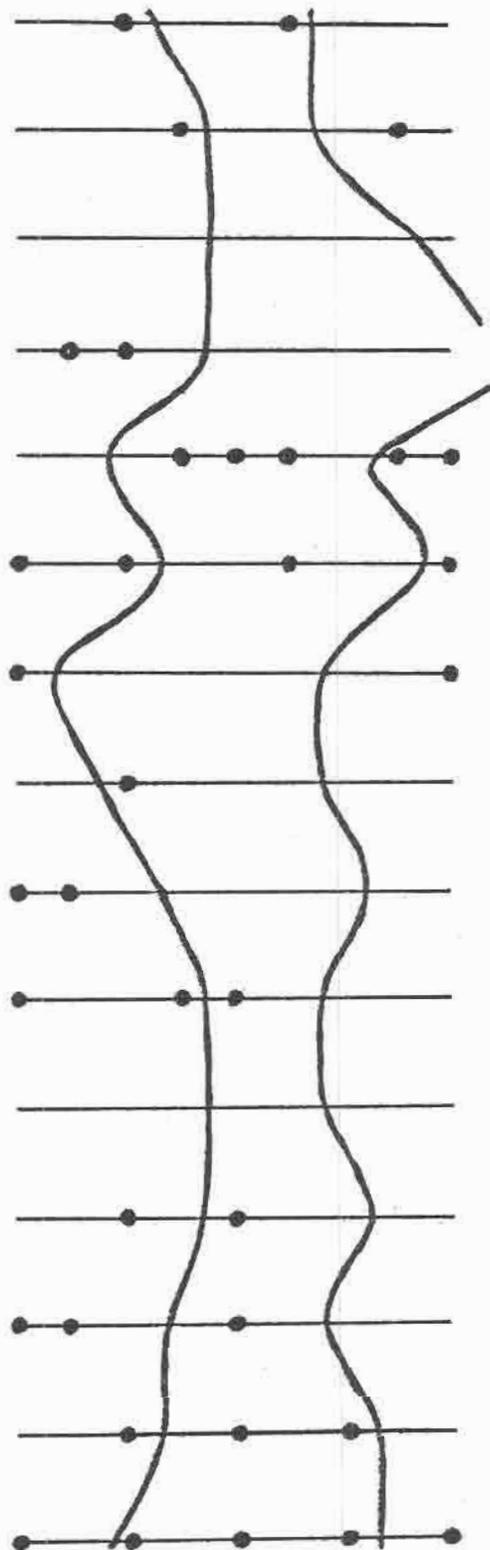


Figure 3. Distribution of capture stations for Peromyscus maniculatus on the Swamper grid. See Figure 1 for further information.

between M. chrotorrhinus and the other two species reflect more specific differences in habitat preference described below.

Patterns of rodent microhabitat use were analyzed in the following manner. The number of trap stations found in each possible category of each habitat variable was tallied. This yielded a frequency distribution (for each variable) of "trap availability" at all possible values of that variable. A similar frequency distribution was computed for trap-stations-of-capture for each rodent species, separately for each habitat variable. Comparison of these two frequency distributions provided a means of testing whether a species was distributed non-randomly across the possible categories of that habitat parameter (i.e., whether it showed a preference for a particular value of that habitat variable). Comparison of the frequency distributions of trap-stations-of-capture for two rodent species allowed testing whether the two species differed in preference for values of each habitat variable. These comparisons were made with chi-square contingency analyses. Data that were initially recorded in "coded" format (i.e., "absence" vs. "presence" or "none" vs. "few" vs. "abundant") were analyzed directly. Data on vegetation density were converted to frequency distributions for these analyses. For percent ground cover and percent canopy closure, 5 equal categories corresponding to 0-20%, 21-40%, etc. coverage were used. For vegetative cover density at 0-1 m and at 1-2 m above ground level, a distribution of 4 equal categories (corresponding to the count of numbers obscured by vegetation) was used. Association of each rodent species with particular species of herbaceous or shrub-layer plants was tested by chi-square.

Data on rodent distribution relative to "structural" habitat variables are shown in Table 4. Standing or running water was found at very few trap

Table 4. Distribution of M. chrotorrhinus, C. gapperi, and P. maniculatus relative to structural habitat variables on the Swamper boulder stream, Cook Co., MN. Data under the column headed "Environment" are the number (in parentheses, proportion) of trap stations present in each category of a habitat variable. Data for each rodent species represent the distribution of trap-stations-of-capture among values of each habitat variable.

<u>HABITAT VARIABLE</u>	Environment	<u>M. chrotorrhinus</u>	<u>C. gapperi</u>	<u>P. maniculatus</u>
BOULDERS				
Absent	36 (.27)	2 (.06)	24 (.27)	12 (.33)
Present	99 (.73)	32 (.94)	65 (.73)	24 (.67)
CREVICES				
Absent	64 (.47)	3 (.09)	41 (.46)	18 (.50)
Few	15 (.11)	3 (.09)	6 (.07)	4 (.11)
Abundant	56 (.41)	28 (.82)	42 (.47)	14 (.39)
SOIL DEVELOPMENT				
None	20 (.15)	12 (.35)	17 (.19)	6 (.17)
Medium	37 (.27)	15 (.44)	22 (.25)	8 (.22)
Good	78 (.58)	7 (.21)	50 (.56)	22 (.61)
MOSS/LICHEN COVER				
None	29 (.21)	2 (.06)	20 (.22)	8 (.22)
Medium	93 (.69)	28 (.82)	61 (.69)	27 (.75)
Thick	13 (.09)	4 (.12)	8 (.09)	1 (.03)
LEAF LITTER				
None	9 (.07)	2 (.06)	8 (.09)	3 (.08)
Scattered	24 (.18)	13 (.38)	16 (.18)	8 (.22)
Thick	102 (.76)	19 (.56)	65 (.73)	25 (.69)
FALLEN TREES/LOGS				
None	27 (.20)	10 (.29)	17 (.19)	3 (.25)
Few	61 (.45)	11 (.32)	42 (.47)	18 (.50)
Abundant	47 (.35)	13 (.38)	30 (.34)	9 (.25)

stations and thus data for this variable were not analyzed. For all habitat variables, the distributions of C. gapperi and P. maniculatus do not differ from each other or from a random distribution in the environment. In fact, both of these species are found in each category of virtually all habitat variables roughly in proportion to availability. This result indicates that these two species have considerable breadth or generality in their microhabitat distribution. In contrast, the distribution of M. chrotorrhinus differed significantly from that of the other species and from a non-random distribution for several habitat variables (all $P < 0.01$). The most striking of these variables are the presence of boulders, the presence of crevices, and the extent of soil development. The association of this species with the exposed boulder field is illustrated by a strong preference for trap stations where boulders were present (94% of trap stations where rock voles were captured) and where at least some rock crevices were available (91% of capture stations). The significantly non-random distribution ($P < 0.0005$) of this species relative to degree of soil development reflects, of course, the fact that little or no soil was present at most sites on the boulder field. Rock voles were also non-randomly distributed relative to leaf litter ($P = 0.035$), avoiding sites with thick litter. The significance of this result, however, is not clear, because leaf-litter thickness was non-randomly distributed between sites where boulders were present vs. absent ($P < 0.002$), with a higher proportion of sites where boulders were absent having thick leaf litter. Like C. gapperi and P. maniculatus, rock voles were randomly distributed with respect to extent of moss/lichen cover and abundance of fallen logs.

These patterns of distribution on the trapping grid are also apparent in relationships with particular plant species. Microtus chrotorrhinus were found at significantly lower-than-expected frequencies in association with wild lily-of-the-valley, thimbleberry, and large-leafed aster (tested by chi-square, all $P < 0.05$). The frequency of occurrence with respect to sarsaparilla was significant at $0.05 < P < 0.10$. These results reflect the fact that these plant species occurred with much greater frequency on portions of the grid with no boulders and good soil development. Red-backed voles were distributed randomly relative to all plants tested. Peromyscus maniculatus showed a significant ($P < 0.05$) "avoidance" of sites with balsam fir seedlings; the explanation for this pattern is not clear.

Frequency distributions of capture sites for the three species are shown in Table 5 for percent ground cover and canopy coverage and in Table 6 for cover density at 0-1 m and 1-2 m above the ground surface. For percent ground cover, the distribution of each species does not differ from the others ($P = 0.13, 0.64, \text{ and } 0.75$, respectively, for comparisons between M. chrotorrhinus and C. gapperi, M. chrotorrhinus and P. maniculatus, and C. gapperi and P. maniculatus). The distributions of C. gapperi and P. maniculatus relative to ground cover clearly do not differ from randomness ($P = 0.97$ and $P = 0.59$, respectively). For M. chrotorrhinus, this probability is $P = 0.067$, indicating a fairly marked departure from a random distribution. The relationship of this species to ground cover density is not totally clear, however. As shown in Table 5, rock voles occur with greater-than-expected frequency at sites with ground coverage of 0-20%, 21-40%, and 61-80% and thus show no consistent pattern across ground cover density. As indicated below, the inconsistency in this relationship is possibly related to the fact that percent ground cover differs between

Table 5. Frequency distribution of capture sites of M. chrotorrhinus, C. gapperi, and P. maniculatus for percent ground cover and percent canopy coverage. See Table 4 for explanation of data presented. Mean values of percent coverage are for non-coded data.

	Environment	<u>M. chrotorrhinus</u>	<u>C. gapperi</u>	<u>P. maniculatus</u>
<u>Ground Cover</u>				
0-20%	36 (.27)	12 (.35)	23 (.26)	11 (.31)
21-40%	29 (.21)	8 (.24)	22 (.25)	8 (.22)
41-60%	33 (.24)	3 (.09)	20 (.22)	5 (.14)
61-80%	26 (.19)	11 (.32)	18 (.20)	10 (.28)
81-100%	11 (.08)	0 (.00)	6 (.07)	2 (.06)
Mean	43%	36%	41%	41%
<u>Canopy Cover</u>				
0-20%	25 (.19)	8 (.24)	21 (.24)	6 (.17)
21-40%	12 (.09)	4 (.12)	11 (.12)	4 (.11)
41-60%	19 (.14)	7 (.21)	11 (.12)	3 (.08)
61-80%	31 (.23)	7 (.21)	17 (.19)	10 (.28)
81-100%	48 (.36)	8 (.24)	29 (.33)	13 (.36)
Mean	60%	52%	55%	63%

Table 6. Frequency distribution of capture sites of M. chrotorrhinus, C. gapperi, and P. maniculatus relative to vegetative cover density at 0-1 m and at 1-2 m above ground level. See Table 4 for explanation of data presented. Cover density codes refer to the mean count of numbers obscured in each stratum on the cover density board as follows: 1 = mean of 1 number obscured; 2 =>1 but<2; 3 =>2 but<3; 4 = 3 to 4.

	Environment	<u>M. chrotorrhinus</u>	<u>C. gapperi</u>	<u>P. maniculatus</u>
<u>Density at 0-1 m</u>				
1	5 (.04)	2 (.06)	4 (.04)	0 (.00)
2	13 (.10)	4 (.12)	11 (.12)	3 (.08)
3	21 (.16)	8 (.24)	15 (.17)	7 (.19)
4	96 (.71)	20 (.59)	59 (.66)	26 (.72)
<u>Density at 1-2 m</u>				
1	13 (.10)	6 (.18)	10 (.11)	2 (.06)
2	23 (.17)	6 (.18)	15 (.17)	7 (.19)
3	30 (.22)	12 (.35)	22 (.25)	9 (.25)
4	69 (.51)	10 (.29)	44 (.49)	19 (.53)

boulder/crevice and other sites. For canopy coverage and both strata of vegetative cover density, the distribution of each species does not differ from the others or from the environmental distribution, although the distribution of M. chrotorrhinus with respect to vegetative cover density at 1 - 2 m approaches significance ($P = 0.104$).

It is of interest to examine whether vegetative characteristics of micro-localities where boulders/crevices are present differ from non-rocky sites. This problem is illustrated by the frequency distributions for each vegetative habitat variable at trap stations where crevices are present and where absent (Table 7). For all vegetative variables, these two distributions are significantly different from each other (for canopy coverage, $P = 0.011$; for the other variables, all $P < 0.005$). In all cases, low-density categories occurred with greater frequency, and high-density categories with lower frequency, at trap stations where crevices are present, indicating that vegetation in these microhabitats is more sparse in all strata.

The problem of vegetative preferences of rock voles can be examined further by factoring out the absence of crevices and comparing patterns shown by rock voles and the other two species only at sites where crevices are present. As described earlier, these trap stations represent over 90% of the M. chrotorrhinus capture sites. Frequency distributions illustrating these patterns are shown in Table 8. For each habitat variable, the frequency distribution of M. chrotorrhinus capture stations does not differ from randomness (all $P > 0.42$) or from the distribution for either of the other two species (all $P > 0.41$). Similarly, distributions for C. gapperi and P. maniculatus do not differ from each other or from a random pattern (all $P > 0.33$).

Table 7. Frequency distributions for vegetative characteristics at trap stations on the Swamper site where rock crevices were present and at those where crevices were absent. See Tables 4 and 6 for explanations of data presented and of cover density codes.

<u>Habitat Variable</u>	<u>Crevices Present</u>	<u>Crevices Absent</u>
Ground Cover		
0-20%	32 (.45)	4 (.06)
21-40%	21 (.30)	8 (.12)
41-60%	10 (.14)	23 (.36)
61-80%	8 (.11)	18 (.28)
81-100%	0 (.00)	11 (.17)
Canopy Coverage		
0-20%	20 (.28)	5 (.08)
21-40%	8 (.11)	4 (.06)
41-60%	9 (.13)	11 (.17)
61-80%	10 (.14)	20 (.31)
81-100%	24 (.34)	24 (.38)
Density at 0-1 m		
1	5 (.07)	0 (.00)
2	13 (.18)	0 (.00)
3	14 (.20)	7 (.11)
4	39 (.55)	57 (.89)
Density at 1-2 m		
1	13 (.18)	0 (.00)
2	16 (.23)	7 (.11)
3	20 (.28)	10 (.16)
4	12 (.31)	47 (.73)

Table 8. Frequency distributions of capture sites for M. chrotorrhinus, C. gapperi, and P. maniculatus relative to vegetative habitat variables at sites where rock crevices were present. See previous tables for further explanation.

<u>Habitat Variable</u>	<u>Environment</u>	<u>M. chrotorrhinus</u>	<u>C. gapperi</u>	<u>P. maniculatus</u>
Ground Cover				
0-20%	32 (.45)	12 (.39)	20 (.42)	8 (.44)
21-40%	21 (.30)	8 (.26)	16 (.33)	7 (.39)
41-60%	10 (.14)	3 (.10)	5 (.10)	0 (.00)
61-80%	8 (.11)	8 (.26)	7 (.15)	3 (.17)
81-100%	0 (.00)	0 (.00)	0 (.00)	0 (.00)
Canopy Coverage				
0-20%	20 (.28)	8 (.26)	16 (.33)	5 (.28)
21-40%	8 (.11)	4 (.13)	8 (.17)	3 (.17)
41-60%	9 (.13)	5 (.16)	6 (.12)	1 (.06)
61-80%	10 (.14)	6 (.19)	4 (.08)	4 (.22)
81-100%	24 (.34)	8 (.26)	14 (.29)	5 (.28)
Density at 0-1 m				
1	5 (.07)	2 (.06)	4 (.08)	0 (.00)
2	13 (.18)	4 (.13)	11 (.23)	3 (.17)
3	14 (.20)	8 (.26)	9 (.19)	5 (.28)
4	39 (.55)	17 (.55)	24 (.50)	10 (.56)
Density at 1-2 m				
1	13 (.18)	6 (.19)	10 (.21)	2 (.11)
2	16 (.23)	6 (.19)	11 (.23)	5 (.28)
3	20 (.28)	11 (.35)	14 (.29)	4 (.22)
4	12 (.17)	8 (.26)	13 (.27)	7 (.39)

Data presented earlier (Table 4) indicate a clear preference of rock voles for micro-localities characterized by the presence of boulders and crevices. However, vegetation density is related to the presence of rocks and rock crevices (Table 7). Thus, it is not immediately clear whether rock voles select boulder sites as a result of the direct significance of rocks and crevices or because of a preference for vegetative configurations associated with rocks. This question was pointed out by Buech et al. (1977) and is critical in our understanding of habitat requirements of this species. Selection of rocky microhabitats on the basis of vegetative attributes would suggest preference for relatively sparse vegetation (Table 7). If that were the case, we would expect to see similar, parallel preferences when only sites with rock crevices are considered. However, data presented in Table 8 do not confirm this expectation. In fact, although the distribution of rock voles across vegetation density does not differ from randomness, the only apparent (but weak) trends in preference of this species are for relatively dense vegetation on the boulder field. This is generally evident in comparisons between the frequency distributions of rock voles and a) the environmental distributions and b) patterns shown by the other two species. The most pronounced trend is for ground cover density, with rock voles occurring at less-than-expected frequencies in the 3 lowest categories and at higher-than-expected frequency at trap stations with 61-80% coverage. Similar but less consistent patterns may be seen for vegetative cover density at 0-1 m and at 1-2 m; there is no consistent relationship to canopy coverage. Similarly, rock voles were found in sparse ground cover categories at lower frequencies, and at 61-80% ground cover at higher frequency, than were C. gapperi and P. maniculatus. For other habitat variables, patterns relative to the other two species are quite inconsistent. Thus, these data

do not indicate that rock voles have a strong preference for sparse vegetation (either absolute or in comparison with sympatric small rodents). This result provides tentative support for the idea that rocks and/or crevices may be directly important as microhabitat features for rock voles.

A perhaps stronger argument in support of this suggestion is derived from comparison of the overall patterns shown by the three rodent species. This argument is based on the facts that 1) nearly all rock vole capture sites were associated with boulders and crevices and 2) frequency distributions of vegetation density in all strata differ strikingly between rocky and non-rocky sites. Thus, if vegetation structure is an important determinant of microhabitat selection by M. chrotorrhinus, we would expect the vegetation preferences of this species to differ from those of C. gapperi and P. maniculatus. However, it cannot be shown that the distribution of rock voles among density categories (for ground cover, "shrub" density, and canopy coverage) differs from that of either C. gapperi and P. maniculatus. This lack of difference is observed whether the entire sampling grid or only the exposed boulder field is considered. Thus, it does not appear that the unique preference of M. chrotorrhinus for rocky microhabitats reflects unique vegetation preferences.

Microclimatic Variables. Our measurements of light penetration at the ground surface indicated no significant difference between rock vole capture sites and control trap stations; this result thus parallels the lack of vegetative differences described above. Results for ambient humidity are of interest because they may shed light on the possible significance of rock crevices for M. chrotorrhinus. Ambient humidity at the ground surface and at 0.5 m above the surface did not differ between selected rock vole capture stations and adjacent control stations (paired t-test, d. f. = 10, $P > 0.25$). However, ambient humidity in crevices

($P=0.0388$, d. f. = 4, including only those control stations where crevices were present) and at the lowest stratum available ($P = 0.0166$, d. f. = 10, including all control stations) was significantly higher at rock vole capture stations. It should be pointed out that this pattern is seasonally dependent, as readings taken later in the autumn failed to indicate a difference between capture and control stations. Thus, although the humidity patterns observed in August must be viewed with caution because they are very time-specific and represent only a few trap stations, they suggest that crevices may be important to rock voles because they provide a moist microclimate. Data on water requirements presently being analyzed by the co-investigator will bear on this problem.

Comparisons with 316 and Brule Sites. The preference of M. chrotorrhinus for rocky microhabitats was apparent on the other two areas, with all rock vole capture sites on the 316 area and 90% on the Brule area characterized by the presence of rock crevices. Analysis of distributions of a large number of boulder diameters ($n = 325$, $n = 197$, and $n = 302$ on the Swamper, 316 and Brule sites) and crevice depths ($n = 234$, $n = 174$, and $n = 276$, respectively) indicated no significant differences in these parameters between the Swamper site and either of the other areas ($P > 0.39$ for diameters; $P = 0.09$ and $P = 0.12$ for crevice depths).

There were several significant differences in vegetation density between the Swamper and 316 or Brule sites. Because of patterns observed on the Swamper area, these comparisons were made using data only from trap stations where rock crevices were present; additionally, this eliminated the effects of differences among areas in proportion of traps placed in boulder areas. Data are shown in Table 9. The frequency distribution of canopy coverage on the Swamper boulder stream did not differ from that at the 316 site ($P = 0.11$) or the Brule site ($P = 0.74$). Vegetative cover

Table 9. Frequency distributions for vegetative habitat variables at trap stations with crevices present on the Swamper, 316, and Brule sites, Cook County, MN. See previous tables for further explanation.

<u>Habitat Variable</u>	<u>Swamper</u>	<u>316</u>	<u>Brule</u>
Ground Cover			
0-20%	32 (.45)	29 (.58)	41 (.56)
21-40%	21 (.30)	15 (.30)	21 (.29)
41-60%	10 (.14)	5 (.10)	8 (.11)
61-80%	8 (.11)	0 (.00)	3 (.04)
81-100%	0 (.00)	1 (.02)	0 (.00)
Canopy Coverage			
0-20%	20 (.28)	21 (.42)	14 (.19)
21-40%	8 (.11)	11 (.22)	8 (.11)
41-60%	8 (.11)	4 (.08)	11 (.15)
61-80%	11 (.15)	5 (.10)	11 (.15)
81-100%	24 (.34)	9 (.18)	29 (.40)
Density at 0-1 m			
1	5 (.07)	6 (.12)	9 (.12)
2	13 (.18)	17 (.34)	11 (.15)
3	14 (.20)	12 (.24)	27 (.37)
4	39 (.55)	15 (.30)	26 (.36)
Density at 1-2 m			
1	13 (.18)	18 (.36)	23 (.32)
2	16 (.23)	13 (.26)	18 (.25)
3	20 (.28)	14 (.28)	26 (.36)
4	22 (.31)	5 (.10)	6 (.08)

density at 0 - 1 m and 1 - 2 m on the Swamper area differed significantly from distributions on the other two areas (for 0-1 m, $P < 0.05$; for 1-2 m, $P < 0.025$). In both cases, the proportion of trap stations in the lowest density category was smaller, and that in the highest density category was larger, on the Swamper boulder stream than at the 316 and Brule areas. A qualitatively similar pattern was observed for ground cover but the difference between Swamper and Brule areas is clearly not significant ($P = 0.31$), that between the Swamper and 316 sites is significant at $P = 0.077$. Thus, in general, ground- and shrub-layer vegetation was more abundant at rocky trap stations on the Swamper boulder stream than at structurally comparable localities on the other two areas.

DISCUSSION AND SUMMARY

This research was designed to examine habitat and microhabitat distribution of Microtus chrotorrhinus in northeastern Minnesota. The Swamper boulder field, where microdistributional patterns were studied, supports rock voles in reasonable and, judging by previous studies (Daniels 1980, Timm 1974, 1975, Timm et al. 1977), stable numbers. This site should thus be regarded as excellent habitat for the species; this likely is a function not only of the structural and vegetative characteristics of the site but also the large extent of the boulder field here.

Analyses of distribution on the live-trapping grid indicate that M. chrotorrhinus was found on or in very close proximity to the exposed-boulder portion of the site; this pattern was reflected in non-random distributions relative to presence of boulders and crevices, degree of soil development, and occurrence of plant species that were found primarily in non-rocky microhabitats. The pattern shown by this species was in striking contrast to those of Clethrionomys gapperi and Peromyscus

maniculatus, both of which occurred in boulder-field traps roughly in proportion to availability. These results indicate that rock voles, at least at this site, are much greater specialists relative to physical habitat structure, and as a result are more restricted spatially than the other two species. This aspect will be considered in more detail below.

Even though density of vegetation at ground, shrub, and canopy levels differs markedly between boulder and non-boulder microhabitats, there is little indication that preference for boulder-associated vegetation structure is a major determinant of M. chrotorrhinus' occurrence on the boulder field. Two major bases for this view were suggested above. First, the vegetation-density preferences of rock voles do not differ from those of C. gapperi and P. maniculatus, and the diversity of density-classes selected by all species was similar. If rock voles select boulder/crevice microhabitats on the basis of vegetative preferences, it is reasonable to expect a) that vegetative preferences of rock voles would differ from those of the other two species or b) that C. gapperi and P. maniculatus would select microhabitats similar to those of rock voles and thus occur with greater frequency on the exposed boulder field than elsewhere. Clearly, neither of these patterns was observed. Secondly, the vegetation preferences of rock voles on the boulder-only portion of the area do not parallel the vegetative differences between crevice-present and crevice-absent sites on the entire grid. Although data on microhabitat distribution at other boulder fields and/or data from manipulative field experiments (especially "habitat tailoring" studies) are needed to conclusively demonstrate this point, it appears that the significance of boulders and/or crevices to rock voles may be direct, rather than indirect through an effect on vegetation density.

Support for this conclusion is provided by the results of a recent survey of rock vole habitats in northeastern Minnesota (Christian 1982) during which over 50 new localities for the species were found. In that study, the presence of boulders and crevices was highly predictive of the occurrence of M. chrotorrhinus. In contrast, density and species composition of vegetation varied tremendously among sites. Those results further suggest that the presence of boulders and crevices may be a more important microhabitat "cue" than any specific vegetative configuration. As pointed out above, the possibility is currently being examined that high moisture levels in those microhabitats, and the relatively high physiological water requirements of M. chrotorrhinus, play a role in that relationship.

The results of this research have important implications for the distribution and long-term stability of M. chrotorrhinus populations, in the context discussed in the introductory section of this report. As noted in that section, many of the known localities for this species in Minnesota are represented by extremely small deposits of boulders (Christian 1982). In the present study, rock voles made very little use of non-rocky microhabitats adjacent to the exposed boulder field at the Swamper site. Similarly, boulders/crevices were present at almost all capture stations for the species at the 316 and Brule sites. If this pattern and degree of habitat specialization are general, many of the known localities for the species must provide extremely limited areas of suitable habitat. This problem is especially critical if, as argued here, boulders and crevices are a directly essential component of rock vole habitat. Thus, data obtained in the present study suggest that 1) as a result of microhabitat specialization, many qualitatively suitable habitats for rock voles in

northeastern Minnesota may be quite small and 2) consequently, many populations of this species in the state may be small, extremely localized, and spatially restricted. Further work on rock voles at smaller boulder-fields is needed, both to determine microdistributional patterns at those sites and, as suggested by Christian (1982), to monitor the long-term stability of these potentially vulnerable local populations.

The above discussion has emphasized consideration of factors that affect presence or absence of rock voles at micro-localities within a given habitat. Another problem concerns differences between or among broadly similar (i.e., rocky) habitats that influence rock vole abundance. The arguments presented above should not be viewed as suggesting that rock voles lack preferences for particular vegetation density profiles but, instead, that their vegetative preferences are 1) similar to those of C. gapperi and P. maniculatus, 2) do not parallel differences between sites where boulders/crevices are present and those where these features are absent, and 3) therefore, cannot be used to explain selection of rocky microhabitats by this species. However, vegetative preferences and the availability of rocky microhabitats with preferred vegetation profiles may explain differences in the abundance of M. chrotorrhinus among sites. Although the patterns of preference observed on the Swamper boulder stream are not entirely clear and are not statistically significant, there is a slight trend - given the presence of boulder/crevices - for rock voles to select microhabitats with relatively abundant ground and shrub layer vegetation. It is rather striking that, at the 316 and Brule sites (where rock voles were less abundant), microhabitats with these vegetation profiles occurred at lower frequency (conversely, low-density categories at higher frequency) than on the Swamper boulder stream. While the

possibility cannot be excluded that other factors, such as boulder field size or configuration, have an effect on density, these results suggest that an abundance of rocky microhabitats with reasonably dense ground and shrub vegetation may be needed to support rock voles at high density.

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