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SELECTION OF MICROHABITAT BY THE RED-BACKED VOLE, *CLETHRIONOMYS GAPPERI*

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Abstract.—*Clethrionomys gapperi* were captured in microhabitats with greater densities of overall cover than at noncapture or random sites within the study area. Variables describing cover density and distance from free water were selected in a discriminant function analysis to differentiate between vole capture and noncapture sites. Vole capture sites had greater amounts of cover within 4 dm above ground surface and were further from standing water than noncapture sites. The preferential use by *C. gapperi* of microhabitats with greater densities of cover is in agreement with laboratory and field assessments of habitat use reported in the literature.

Gapper's red-backed vole occurs in forests of the Hudsonian and Canadian life zones. It occurs chiefly in coniferous, deciduous, and mixed forests but sometimes occurs in cutover areas or blowdowns. Its presence appears to be associated with abundant litter of stumps, rotting logs, exposed roots, and a dense leaf litter. Its diet consists of hypogeous fungi, vegetation, seeds, insects, and other invertebrates (Merritt 1981). The abundance of red-backed voles has frequently been reported to be related to moist habitats (Gunderson 1959, Getz 1969, Kirkland and Griffin 1974, Miller and Getz 1977, Merritt and Merritt 1978, Mihok 1981, Vickery 1981) and dense cover (Lovejoy 1975, Kirkland 1977, Miller and Getz 1972, 1973, Gunther et al. 1983). The relationship between cover density and vole occurrence, however, has not been well quantified.

We made a statistical analysis of the relationship between the abundance of red-backed voles and characteristics of the habitat as part of a study to investigate the relationship between habitat structure and predation in red-backed voles and deer mice, *Peromyscus maniculatus* (Wywialowski 1987). To assess the importance of habitat attributes to red-backed vole abundance, we compared capture sites with noncapture and random sites (Williams 1983). Habitat variables reported as important to *C. gapperi* by other studies (Johnson 1981) were selected a priori for this study.

Study Area

The study site was south of the South Sink on the Cache National Forest in northern Utah. The site ranged from 2,370 to 2,380 m elevation and had a prevailing northerly aspect. The trapping area was dissected by numerous small streams and seeps. A mixture of habitats occurred on the site ranging from a small, open meadow to mature forest. The site was dominated by subalpine fir, *Abies lasiocarpa*, with Engelmann spruce, *Picea engelmannii*, Douglas-fir, *Pseudotsuga menziesii*, lodgepole pine, *Pinus contorta*, and quaking aspen, *Populus tremuloides*, also present. The dominant "shrub" was subalpine fir seedlings, and a variety of forbs were present. See Schimpf et al. (1980) for a detailed description of the area.

Methods

Livetraps were placed in a grid pattern on 10 July 1983. The trapping grid was located in an area where *C. gapperi* had been successfully captured the previous fall. Traps were spaced approximately 15 m apart and were set in what was judged to be the best potential vole capture microsite within a 9-m^2 area centered on each grid node. The traps were baited with a mixture of oatmeal and peanut butter and set on 13 July 1983. Traps were checked the following morning, evening, and the next morning, at which time they were closed. All voles were removed from the site

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for use in a laboratory experiment (Wywialowski 1987), while other rodent species were released. The same procedures were followed starting on 11 August and on 5 October 1983, except that during the second session both deer mice and voles were removed.

To determine the range of the habitat attributes available to voles, we selected 70 random points within the trapping area. These points were chosen by randomly locating a point in the northeast quadrant of the study area and systematically spacing the remaining 69 points across the study area.

Habitat structure, including composition of horizontal cover, plant species composition, and physical attributes, were recorded at each of the 101 trap sites and 70 random points within the trapping area (Table 1). Measures of habitat structure were taken within a 1-m radius of each trap site or random point. Cover density was estimated at 10-cm intervals up to 1 m by visually aggregating the cover and estimating the percent of the total area, similar to the methods used in habitat typing (Steele et al. 1981). The amount of cover was recorded as: none, trace to 5%, 5–15%, 15–25%, through 85–100%. Percent of horizontal cover was measured by line-intercept on two 2-m transects centered on the trap to estimate the amount of standing tree, downed wood, rock, evergreen or deciduous shrub, and herbaceous cover. Tree overstory was measured by summing five ocular sightings of the canopy (recorded as 0 = sky or 1 = blocked by trees, with a sighting over the trap and at both ends of the two transects). Nearest tree, shrub, and herbaceous species were recorded. Physical factors measured included distance to, diameter of, and age class of the nearest downed wood; depth of duff (to mineral soil); and distance to nearest free water.

Analysis of the data was done using SPSSx, the Statistical Package for the Social Sciences (SPSS Inc. 1983). Sites where a single juvenile male was captured (n = 7) were not included in the analysis because this group of voles ranks at the bottom of the dominance hierarchy of sex and age classes (Mihok 1981), and the animals were most likely to occupy suboptimal microhabitats. Therefore only 94 trapping sites were used in the analysis.

Differences between random, noncapture, and capture sites were tested using t-tests for differences between trap and random sites, Kendall's Tau for comparisons of habitat attributes between capture and noncapture sites, and Chi-square for determining whether plant species presence was related to vole capture and noncapture sites (Hollander and Wolfe 1973).

Discriminant function analysis (DFA) was used to assess the ability to predict vole capture or noncapture sites based on the habitat structure at the trap sites. Prior probabilities were set at size of the groups to minimize any sample-size bias (Titus et al. 1984).

TABLE 1. Habitat variable names and their descriptions.

Name	Description
CD1-CD10	Percent of cover density within a meter radius of the site at 0–10 to 90–100 cm above ground, respectively.
CLOW	Mean of the values from CD1 through CD3.
CMID	Mean of the values from CD4 through CD7.
CHIGH	Mean of the values from CD8 through CD10.
CSUM	Mean of the values from CD1-CD10.
SHRUB	Percent of cover composed of shrubs within a 1-m radius of the site.
FORB	Percent of cover composed of forbs within a 1-m radius of the site.
GREEN	Sum of SHRUB and FORB.
WOODY	Percent of cover composed of downed woody material within a 1-m radius of the site.
TREE	Percent of area composed of standing tree trunks within a 1-m radius of the site.
CANOPY	Percent of five measurements at the site and 1 m from the site in the four cardinal points.
DUFF	Depth of organic material to mineral soil in cm.
WATER	Distance to nearest open water in m.
LOG-DIST	Distance to nearest log greater than 1 dm in cm.
LOG-SIZE	Size of nearest log greater than 1 dm in diameter in cm.
LOG-CLASS	Age of downed logs rated on a scale of 1 = freshly fallen to 5 = mostly decayed after Thomas (1979).

TABLE 2. Means and standard errors of cover and habitat variables for random, vole capture, and vole noncapture sites.

	Sites					
	Random n = 70		Vole noncapture n = 41		Vole capture n = 53	
Variables	x	SE	x	SE	x	SE
CD1	27.2	3.0	56.0	4.1	60.5	6.1
CD2	16.5	2.5	43.9	3.7	50.7	3.9
CD3	11.8	2.2	33.1	3.2	40.8	3.2
CD4	8.9	1.9	24.9	2.8	32.5	2.9
CD5	7.2	1.7	19.5	2.4	25.2	2.5
CD6	5.9	1.6	15.7	2.1	19.1	1.9
CD7	5.0	1.4	13.9	2.1	16.3	1.5
CD8	3.8	1.2	11.9	1.8	14.6	1.5
CD9	3.6	1.2	11.6	1.8	12.4	1.2
CD10	3.4	1.2	11.4	1.8	10.9	1.1
CLOW	14.0	2.1	44.3	4.3	50.7	3.4
CMID	7.0	1.6	18.5	2.2	23.3	2.0
CHIGH	4.0	1.3	11.6	1.8	12.7	1.2
CSUM	9.0	1.6	24.8	2.2	28.9	1.9
SHRUB	13.2	3.0	34.0	5.0	41.1	4.8
FORB	27.1	4.1	10.9	2.7	13.1	2.9
GREEN	40.2	4.3	45.0	5.5	54.1	4.7
WOODY	8.4	2.0	12.0	2.1	11.5	1.9
TREE	0.7	0.3	3.8	0.9	2.1	0.6
CANOPY	45.0	4.1	74.0	4.2	57.0	9.0
DUFF	6.3	0.8	12.2	1.3	12.1	1.7
WATER	12.0	1.5	15.2	2.8	20.9	2.2
LOG-DIST	141.8	16.6	49.4	13.6	54.5	11.2
LOG-SIZE	18.3	2.0	24.1	3.5	21.3	2.3
LOG-CLASS	2.3	0.1	3.0	0.2	2.5	0.2

TABLE 3. Tests for ordered relationships between vole capture (n = 53) and noncapture (n = 41) sites with respect to the habitat variables at the trapsites. * = $P \leq .05$, ** = $P < .01$.

Variable	Tau c value	Significance level
CD1	0.107	0.169
CD2	0.167	0.063
CD3	0.185	0.057
CD4*	0.189	0.052
CD5	0.149	0.099
CD6	0.152	0.092
CD7	0.162	0.079
CD8*	0.201	0.040
CD9	0.150	0.092
CD10	0.096	0.197
CLOW	0.125	0.138
CMID*	0.201	0.029
CHIGH	0.058	0.243
CSUM	0.088	0.216
SHRUB	0.106	0.172
FORB	0.035	0.373
GREEN	0.103	0.220
WOODY	−0.016	0.445
TREE**	−0.252	0.004
CANOPY	−0.099	0.193
DUFF	−0.061	0.296
WATER**	0.278	0.009
LOG-DIST	0.151	0.094
LOG-SIZE	−0.071	0.268
LOG-CLASS	−0.145	0.089

RESULTS

Over the three trapping sessions 119 red-backed voles were captured during 593 trapnights. Capture success averaged 20 voles per 100 trapnights.

Microhabitat differed among vole capture, noncapture, and random sites. The mean percentage of cover for all trap sites (capture and noncapture) was greater than the mean percentage of cover for the trapping area, as sampled by random points within the trapping grid ($t = 7.95$, $P < .001$, Table 2). Voles were captured at sites that had more cover than noncapture sites for the mean cover density from 30 through 70 cm (CMID, Tau c = 0.201, $P = .029$, Table 3). Eight of the 10 cover density variables (all except the bottom and top 1 dm) were significantly positively related at $P < .10$. Vole capture sites were less likely to be near trees (Tau c = −0.252, $P = .004$) and were farther from water than noncapture sites (Tau c = 0.278, $P = .009$, Table 3).

TABLE 4. Nearest tree to sites. Actual number and percent of the total for the study area given for random and trap sites. Observed and expected numbers are given for vole capture and noncapture sites.

Site		Tree species				
		Abies lasiocarpa	*Picea engelmannii*	*Pinus contorta*	*Populus tremuloides*	Total
Random	(n)	20	28	6	14	70
	(Percent)	28.6	40.0	8.6	20.0	97.1[a]
Trap	(n)	42	30	7	15	94
	(Percent)	44.7	31.9	7.4	16.0	100.0
Noncapture	(n)	16	15	5	5	41
	(Expected n)	18.3	13.1	3.1	6.5	
Capture	(n)	26	15	2	10	53
	(Expected n)	23.7	16.9	3.9	8.5	

[a]Two (2.9%) random sites had no tree within 5 m.

TABLE 5. Nearest shrub to sites. Actual number and percent of the total for the study area given for random and trap sites. Observed and expected numbers are given for vole capture and noncapture sites.

Site		Shrub species				
		Abies lasiocarpa	*Picea engelmannii*	*Pinus contorta*	*Populus tremuloides*	Total
Random	(n)	32	0	9	15	70
	(Percent)	45.7	0.0	12.9	21.4	79.3[a]
Trap	(n)	66	4	8	16	94
	(Percent)	70.2	4.3	8.5	17.0	100.0
Noncapture	(n)	29	2	4	6	41
	(Expected n)	28.8	1.7	3.5	7.0	
Capture	(n)	37	2	4	10	53
	(Expected n)	37.2	2.3	4.5	9.0	

[a]Fourteen (20.7%) random sites had no shrub within 5 m.

Capture sites were not associated with the species of the nearest tree ($X^2 = 3.86$, 3 d.f., $P = .28$, Table 4), the nearest shrub ($X^2 = 0.45$, 3 d.f., $P = .93$, Table 5), nor the nearest forb ($X^2 = 0.92$, 4 d.f., $P = .92$, Table 6).

The discriminant function analysis selected cover density from 3 to 4 dm above ground, distance from water, and number of trees within 1 m of the trap as the variables to distinguish between vole capture and noncapture sites (Table 7). Using these three variables, we correctly classified 65% of the sites as capture or noncapture sites. More errors in classification occurred for the noncapture sites (54% were classified as capture sites), whereas 78% of the capture sites were correctly classified. If only vole captures from the first nights of trapping were included in the discriminant analysis, 80% of the sites were correctly classified (76% of the capture sites and 95% of the noncapture sites).

DISCUSSION

The density of cover and the structure of the vegetation were important (Table 3) in determining probable capture sites of red-backed voles. Vole capture sites had high values of cover density through the 1-m height (Table 3). The cover density from 3 to 4 dm above the ground was the most important variable distinguishing between vole capture and noncapture sites (Table 7). Voles used areas of dense, and appeared to avoid areas with sparse, ground cover. Miller and Getz (1973) found *C. gapperi* to be more abundant in areas with shrub cover greater than 50%, herb cover greater than 25%, and debris cover greater than 25%. Similarly, California red-backed voles, *Clethrionomys californicus*, were negatively associated with the amount of light reaching the forest floor and the amount of ground vegetation (Maser et al. 1981) and

TABLE 6. Nearest forb to sites. Actual number and percent of the total for the study area given for random and trap sites. Observed and expected numbers are given for vole capture and noncapture sites.

	Forb species					
Site	*Arnica* spp.	*Ranunculus* spp.	*Osmorhiza* spp.	*Thalictrum* spp.	Other	Total
Random (n)	12	5	16	0	37	70
(Percent)	17.1	7.1	22.9	0.0	52.9	100.0
Trap (n)	27	11	17	7	32	94
(Percent)	28.7	11.7	18.1	7.5	34.0	100.0
Noncapture (n)	13	5	8	2	14	42
(Expected n)	12.1	4.9	7.6	3.1	14.3	
Capture (n)	14	6	9	5	18	52
(Expected n)	14.9	6.1	9.4	3.9	17.7	

TABLE 7. Classification function and discriminant coefficients for vole capture and noncapture sites.

	Classification function		
Variables	Group 1 (Capture)	Group 2 (Noncapture)	Discriminant function
CD4	0.101	0.076	0.025
WATER	0.101	0.076	0.025
TREE	0.089	0.146	−0.058
Constant	−2.641	−3.368	6.009

thus, presumably, positively associated with canopy. In contrast with *C. californicus*, green vegetation and canopy coverage were not associated with the presence of *C. gapperi* in this study (Table 3), nor was the close association found by Maser et al. (1981) of California red-backed voles with rotting and punky logs (class 3 or more; see Table 1 for definition of classes) true for *C. gapperi* in our study. In fact, *C. gapperi* capture sites were positively associated with more recently fallen class 2 logs (Table 3). While releasing voles in the field, we observed that they frequently ran along or under class 2 logs. Because class 2 logs are still above the ground surface in some places, they provide a secure travel lane for voles. Class 3 or older logs usually cannot function the same way. Fewer class 2 logs may have been present on Maser et al.'s (1981) plots than in this study. Olszewski (1968) reported that the bank vole, *Clethrionomys glareolus*, traveled under fallen timber, a behavior that appears similar to that which we observed for red-backed voles.

Distance from water was significantly different between vole capture and noncapture sites (Tables 3 and 7). Voles were captured farther from water, on a relative scale within the study site (Table 2). Voles in captivity are dependent on free water (Odum 1944, Getz 1968), unless their food is very succulent (personal observation). In Connecticut, the southern portion of the geographic range in the northeastern USA, *C. gapperi* were restricted to swampy areas, but in Vermont, farther north, voles acquire adequate water from their food (Miller and Getz 1972).

Voles in this study were captured relatively far from water; if they were too close, their burrows could have been flooded by the frequently fluctuating water levels in the study area. For example, Merritt and Merritt (1978) found that the spring snowmelt was the period of greatest mortality for a Colorado subalpine population of *C. gapperi*. The greatest density of voles was close to a creek within their study plot.

Although distance from water is not equivalent to distance above water level, given the topography of the study area, a strong positive relationship is likely. Voles should not have occurred within our study area immediately near water. Only distances from 0 to 45 m from water were sampled in this study, resulting in the positive relationship observed. If sites further from water had been sampled, fewer voles would likely have been captured. Prior investigations of vole densities on drier sites within close proximity of the study site captured few (Anderson et al. 1980) or no voles (personal observation). Additionally, voles within our moist study site may not have been dependent upon free water, as the site may have provided sufficient moisture through the vegetation to meet vole requirements.

The number of trees in the area was the

third variable chosen (Table 7). Voles were more likely to be captured within the study area at sites with fewer trees present. This is consistent with vole selection of microhabitat sites with greater amounts of cover. Many of the trees within the study area were mature trees with large bole diameter. These trees had little cover 0 to 4 dm above ground in the areas immediately surrounding their bases.

The relationship of red-backed voles to the presence of free water illustrates a problem that exists with all studies, similar to ours, that use correlation analysis to investigate relationships of habitat and animal abundance. As demonstrated by Price and Kramer (1984), the location selected by researchers for their traps can influence the conclusions drawn about habitat affinities of a species. In our case, (1) locating the trapping grid in an area with a wider moisture gradient would have resulted in a different statistical relationship between vole density and distance to free water, and (2) placing the traps in random locations on the trapping grid would have increased the significance between vole abundance and habitat attributes. In order to meet objectives other than those reported here, however, we located traps at sites we believed most likely to catch voles. As a result, trapping sites did not encompass the full range of values for most of the habitat attributes (Table 2). Random or stratified random placement of traps would have resulted in relationships that were statistically more significant for all variables (Table 3), but use of a random design would not have changed our conclusions as to the importance of the currently significant cover variables. It would have made the relationships between variables more significant and perhaps would have resulted in less significant ($P > .05$) variables becoming significant. The variables most likely to have changed would be other density (CD2-CD9) and the log-class variables.

Floristic composition was not important in determining whether or not a vole was captured at a site (Tables 4, 5, 6). Similar analyses have not been reported for *Clethrionomys* but have been reported for other rodent species (e.g., *Peromyscus leucopus*, M'Closkey and Lajoie 1975).

Researchers studying small mammals and their habitats usually assume that capture location is indicative of preferred or most used habitats (Dueser and Shugart 1979). The correlation of *C. gapperi* with cover density described here agrees with the laboratory preference of the species for more cover (Wywialowski 1987) and use of microhabitats with greater cover as assessed by radiotelemetry in a forest enclosure (Nams 1981).

The habitat in which an individual occurs in a field situation is always confounded by the presence of other animals. Dispersers and subordinate animals are more likely to be in suboptimal habitats. Density may be a poor indicator of habitat quality (Van Horne 1983). Van Horne (1982) found that dominant adult deer mice occupied forest habitats with greater cover and had higher overwinter survival, while subordinate subadults occupied habitats with less cover where densities were higher but overwinter survival was less. A similar pattern of use between adult and juvenile *C. gapperi* in a forest and tornado blowdown, respectively, was observed by Powell (1972), although he did not have any measure of fitness of individuals within each habitat. Mihok (1981) found that mature females were dominant and occupied preferred habitats. In this study, 8 of the 14 voles captured the first night of the first trapping period were females, whereas only 2 of the 10 captured the second night were female. The sex-biased captures concur with the female-dominated social organization of the genus *Clethrionomys* (Mihok 1981, Bujalska 1985, Vitala and Hoffmeyer 1985, Bondrup-Nielson 1986a, 1986b). Many territorial females were likely removed the first night of trapping. The pattern of capture of mostly adult female voles during the first night of trapping was not as prevalent during the second and third trapping periods, when mostly young-of-the-year voles were captured and territories and social order were likely disrupted by the previous removal of voles. The effect of social organization on our conclusions is not completely clear. It did, however, affect our ability to correctly classify the habitat use of voles. When only the first trapnights were used in the analysis and trapped voles consisted mostly of adults, 80% of the sites were correctly classified. When the second trapnight consisting of mostly juvenile voles was added, only 65% of the sites were correctly classified. The major difference between the two analyses appears to be in the importance of cover below the 4-dm height. We conclude that optimal vole habitat has high values of cover below 4 dm.

Population size may also affect habitat use by a species. Bock (1972) found that *C. glareolus* occupied a wider range of habitats when populations were larger. This may not be true for *C. gapperi*, as they have been reported not to have exhibited significant opportunistic niche expansion in one study on an island situation (Crowell 1983). However, microhabitats that were preferentially used in this study are in agreement with the laboratory research of Wywialowski (1987) and the field observations of Nams (1981). Capture rates of red-backed voles in other studies have averaged 0.7–8.7 captures per 100 trapnights (Gunderson 1959, Martell 1981, Gunther et al. 1983, Fuller 1985), except for Martell's (1983) study where snap-trap capture rates as great as 37.8 per 100 trapnights were obtained. The capture rate of 20.1 captures per 100 trapnights observed during our study, excluding Martell (1983), is about an order of magnitude greater than the average capture rate reported elsewhere for red-backed voles. Vole captures in this study probably occurred in suboptimal as well as optimal habitats, and, as a result, our ability to identify what constitutes optimal vole habitat is more difficult than it would have been if vole populations had been lower.

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