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Home range and habitat affinity of the singing vole on the North Slope of Alaska

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A B S T R A C T

A species' use of space provides insight into fundamental resource requirements and population dynamics. Here we investigate how microhabitat features and intraspecific interaction contribute to space use by the singing vole (*Microtus miurus*) on arctic tundra. We used mark-recapture of singing voles to estimate home range using a kernel density estimator. To assess intraspecific interactions, regions within home ranges were classified as “exclusive” or “shared” based on overlap among individuals. The spatial distribution of singing vole encounters was analyzed in conjunction with multivariate hierarchical cluster analysis of vegetation cover to assess microhabitat affinity. “Shared” regions within home ranges were used more than expected based on proportional availability. We observed significant affinities for microhabitats at both the scale of individual home ranges and of the singing vole population. Our results suggest that heterogeneity in microhabitat features and social interactions are important factors in structuring singing vole space use. These results have implications for the impact of singing vole activity on tundra plant communities and for the resilience of the singing vole and other arctic microtine rodents to stochastic climatic conditions.

INTRODUCTION

The dynamics of space use are important for comprehensive analysis of the responses of small mammals to resource availability, including habitat features and interactions between individuals. An individual's home range provides a measure of space use and may be affected by population density, social organization, and competition (Swingland and Greenwood, 1983; Krebs, 2013). Systems dominated by a single species can provide an excellent framework for understanding home range by removing the confounding effects of interspecific competition for shared diet and habitat resources. The size and placement of small mammal home ranges are conducive to assessing microhabitat affinity, whereas overlap among home ranges can define the spatial resolution of intraspecific interactions. A clearer understanding of

the factors influencing space use can inform assessments of the resilience of species to changing environmental conditions, which is of particular importance for fauna on the rapidly warming arctic tundra.

The singing vole (*Microtus miurus*), a Nearctic microtine rodent (subfamily Arvicolinae; e.g., voles and lemmings), is well suited for examining space use dynamics. Singing voles occur primarily on well-drained tundra in northern Alaska in the U.S.A., and northern Yukon and westernmost Northwest Territories in Canada. The northern foothills of the Brooks Range, Alaska, is a treeless region underlain by continuous permafrost with a mosaic of tundra plant communities. Here, the singing vole is one of five species of microtine rodents, all of which are herbivorous. The singing vole and the root (or tundra) vole (*M. oeconomus*) are codominant species, whereas the northern

red-backed vole (*Myodes rutilus*), the collared lemming (*Dicrostonyx groenlandicus*), and the brown lemming (*Lemmus trimucronatus*) are present but rare (Bee and Hall, 1956; Batzli and Henttonen, 1990). In contrast to the root vole, which has been extensively studied across its Holarctic range (Batzli and Henttonen, 1990; Andreassen et al., 1998; Hovland et al., 1999), the singing vole has been less extensively studied. These congeners exhibit limited ecological overlap, as they segregate spatially across habitats along a moisture gradient: the singing vole prefers mesic (i.e., well-drained) habitats, and the root vole prefers wet-moist (i.e., poorly drained) habitats (Galindo and Krebs, 1985; Batzli and Henttonen, 1990, 1993; Batzli and Lesieutre, 1991, 1995; Maguire, 2015). Because of this spatial segregation, population dynamics of the singing vole can be examined without the confounding effects of competitive interactions with other herbivorous rodents. Although other small mammals (e.g., shrews and diurnal arctic ground squirrels) may occur at low density in mesic tundra, differences in diet, activity time, and habitat requirements suggest that local interactions among these species are unlikely to play a strong role in structuring individual space use.

Notably, the singing vole is unique among microtine rodents in its tendency to both cooperatively build haypiles aboveground as a winter food source (Batzli and Henttonen, 1993) as well as cache food belowground (Cole and Wilson, 2010). These behaviors underscore the importance of characterizing habitat affinities that may facilitate food provisioning and quantifying shared space use. Moreover, an improved understanding of space use is valuable in addressing questions on the impacts of stochastic winter weather events on singing vole population dynamics, which may not be uniform across microtine rodent habitat types (Duchesne et al., 2011; Bilodeau et al., 2013).

We report the findings of an intensive mark-recapture survey of singing voles on rocky floodplain tundra habitat near Toolik Field Station, located on the northern foothills of the Brooks Range. Our objectives were to (1) document annual variation in singing vole space use related to population density; (2) assess size, overlap, and intensity of use within core areas of singing vole home ranges; and (3) assess microhabitat affinity of the singing vole at both the population and individual level. These analyses inform our understanding of the role of microhabitat features and social interaction in structuring singing vole space use. We discuss our findings within the context of small mammal population dynamics and the consequences of habitat changes to arctic ecosystems.

METHODS

Field Surveys

Field surveys were conducted on the northern foothills of Alaska's Brooks Range near Toolik Field Station (TFS) (68°38'N, 149°36'W at 720 m a.s.l.) in 2013 and 2014. In June 2013, a mark-recapture grid was established on a rocky floodplain near the outlet stream of Toolik Lake (Fig. 1). This location was chosen based on prior sampling in the 1980s by Batzli and colleagues (Batzli and Henttonen, 1990, 1993; Batzli and Lesieutre, 1995). The grid was 0.42 ha in extent, composed of four parallel trap-lines with a trap station set every 10 m for a total of 60 stations across the 30 m × 140 m array. Two Sherman live traps (H. B. Sherman, Tallahassee, Florida, U.S.A.) were baited with peanut butter and set to rodent sign (e.g., latrine, runway, grazed vegetation) within 2 m of each trap station, for a total of 120 traps. Three discrete sampling sessions were conducted during the summers of 2013 and 2014: in early June following snowmelt, in July about peak green-up, and in August during plant senescence. In each session, sampling was conducted for four consecutive nights. Traps were checked approximately every six hours (midnight, morning, midday, evening) to reduce incidental mortality. Across each summer season the grid was surveyed for 1440 trap-nights, with a total of 5040 trap-checks.

Upon capture each individual was identified to species, sexed, aged (juvenile, subadult, adult), examined for reproductive condition, weighed (using a Pesola® scale), and marked with a Passively Integrated Transponder tag (Biomark, Boise, Idaho, U.S.A.). Weight was used to place individuals in one of three age categories: juvenile (all individuals ≤ 18 g), subadult (females 18–28 g; males 18–30 g), and adult (females > 28 g; males > 30 g) (Myllymäki, 1977; Batzli and Henttonen, 1990, 1993). Field procedures follow guidelines of the American Society of Mammalogists (Sikes, et al., 2011) and were approved by the University of New Hampshire Animal Care and Use Committee (protocol 130205).

Vegetation sampling was conducted at each of the 60 trap stations in July 2013 (during peak growing season). Using a 1 m × 1 m quadrat at each trap station, cover was recorded (under the Daubenmire method: <5%, 5–25%, 25–50%, 50–75%, 75–95%, 95–100%) for each of nine functional types: bare, litter, lichen, moss, *Equisetum* spp., graminoid, forb, evergreen shrub, and deciduous shrub. Vegetation cover data were assumed to be representative of the area surrounding each trap station.

Concurrent with these surveys, mark-recapture grids were established on five additional tundra plant communities near Toolik Lake, spanning the available mois-

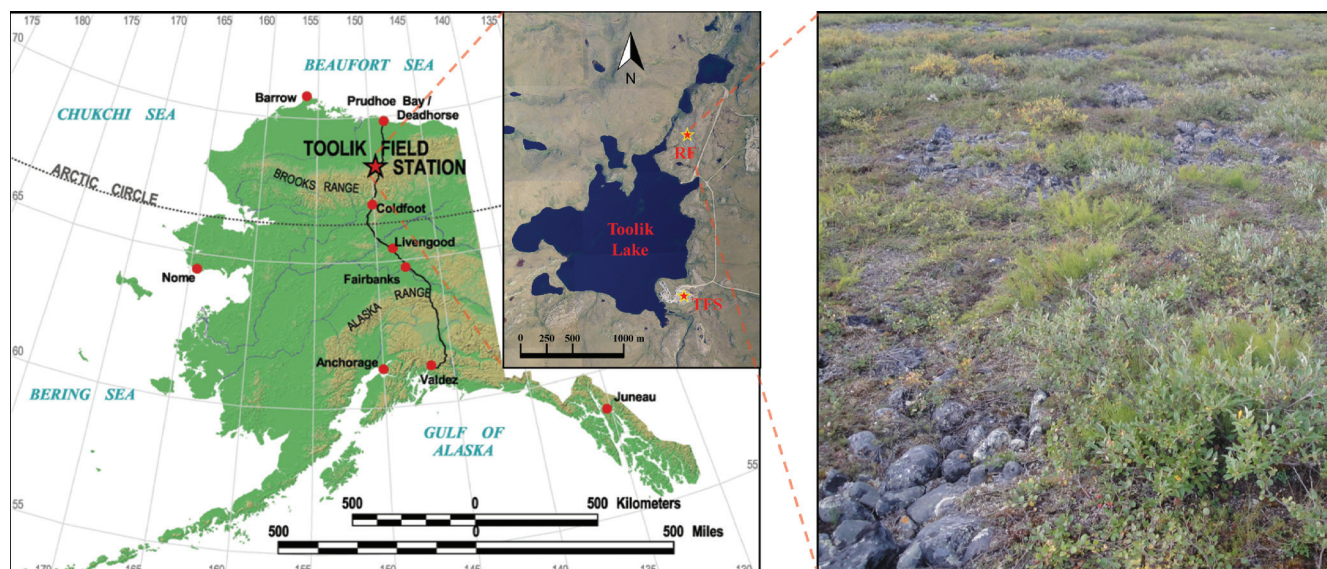


FIGURE 1. Locations of 0.42 ha rocky floodplain grid (RF), Toolik Lake, and Toolik Field Station (TFS) (inset) in Alaska (left panel). Base map provided by Toolik Field Station GIS Department. The photograph (right panel) provides an example of the mosaic of microhabitats on the rocky floodplain.

ture gradient (Maguire, 2015). In addition to the rocky floodplain discussed here, singing vole populations occurred on two other mesic habitats (moist nonacidic tundra and mesic heath); however, those sample sizes were insufficient for assessment of space use (Maguire, 2015).

Population Density Estimation

Abundance (i.e., population size) of singing voles was estimated using a robust design Huggins closed-captures model (Huggins, 1989) in program MARK (Cooch and White, 2015). Abundances were estimated separately for each of three sampling sessions (June, July, August) in each year (2013 and 2014). The Huggins closed-captures model operates under the assumption that the sample population was closed (i.e., no temporary immigration, emigration, births, or deaths) during each session. This is a reasonable assumption given that sampling sessions were limited to four consecutive nights, and comparisons made based on abundance estimates among sessions are relative. Encounters (i.e., captures) of each individual were aggregated within each day and converted to binary values, such that daily encounter histories across the summer season for all individuals were used in the Huggins closed-captures model. In calculating the effective area, we included a boundary strip beyond the extent of the grid. For each year, the boundary strip was calculated as half the mean of the maximum distance moved by the sample population (Otis et al., 1978; Krebs et al., 2011). Density was estimated by dividing abundance

estimates for each month by the effective area sampled in the given year.

Home Range Estimation and Analysis

Relocation data from all three sampling sessions were aggregated for each individual and home range analysis was conducted for each vole encountered ≥ 5 times within a sampling year (Batzli and Henttonen, 1993). A linear regression was used to test whether home range area increased with number of relocations used for estimation. Only the space use of female singing voles was modeled due to the documented instability in home range size and placement of male singing voles as they shift across the landscape during the summer breeding season (Batzli and Henttonen, 1993). Moreover, we did not document a sufficient sample size of males with the requisite ≥ 5 recaptures to incorporate a sex-comparison into our analyses. Only individuals recorded as subadult or adult (based on age class in month of final relocation) were included in the analysis to avoid modeling artificially small home ranges of recently weaned juveniles. Aggregating encounters over the breeding season ensured that any short-term change in space use due to pregnancy, lactation, or emergence of juveniles would not bias the home range estimate.

Home range models were constructed using kernel density approaches in the 'adehabitatHR' package (Calenge, 2006) in R (R Core Team, 2015). Minimum convex polygons (MCPs) were also constructed solely to facilitate comparison with singing vole home range

estimates calculated by Batzli and Henttonen (1993) from this site using data from the 1980s. A kernel density estimator (KDE) was used to model utilization distributions (UDs) for each vole. The UD displays the probability density of relocating a vole given coordinates (Van Winkle, 1975; Silverman, 1986; Seaman and Powell, 1996). Unlike MCPs, UD is robust to spatial autocorrelation (de Solla et al., 1999; Barg et al., 2005; Hoset et al., 2008). A fixed kernel was used with the reference bandwidth (h_{ref}), which is best for analyzing the internal structure within UD (Seaman and Powell, 1996; Vander Wal and Rodgers, 2012). The bandwidth determines the width of the kernels placed over relocation coordinates and controls the smoothing of the UD based on the proximity of other relocation points (Silverman, 1986; Seaman and Powell, 1996; Vander Wal and Rodgers, 2012).

Home ranges were delineated from each UD by the 95% isopleth (Vander Wal and Rodgers, 2012), reflecting a conservative estimate of the entire area used by each singing vole. Because home range is an ambiguous term, a refined and more biologically relevant core area was delineated following Vander Wal and Rodgers (2012). By using a probability density function, the core area is defined objectively as the region of the home range where the probability of occurrence is greater than expected under uniform use (Samuel et al., 1985; Barg et al., 2005; Vander Wal and Rodgers, 2012); this approach is standardized and repeatable. Derivation of core area was done by plotting the UD area against the UD volume, resulting in an exponential relationship. UD area corresponds to the size of the region constrained by a probability density isopleth (% of activity contained) of the UD volume. The area axis was standardized proportional to the total area covered by the 95% UD isopleth ($0 \leq \text{total area} \leq 1$), which made it congruent to the volume axis, plotted as UD volume isopleths ($0 \leq \text{UD}$

volume ≤ 1). Core area was defined by determining the point at which the slope of the curve of best fit equals 1 (set the first order derivative to 1); the area within the corresponding isopleth represents the core area where the individual's activity was maximized (Fig. 2). The individually calculated isopleths ($n = 17$) for each vole were similar ($60.9 \pm 0.19\%$), so for simplicity the mean value (61%) was used as the core area isopleth for all voles.

To verify that the region delineated by the 61% isopleth was indeed functionally used as the core area, intensity of use was calculated following Samuel et al. (1985) and Vander Wal and Rodgers (2012) by dividing the core isopleth (61%) by the proportion of total area represented as core. Values for all core areas were >1 , confirming that the core area was used more intensely than the periphery. Additionally, percent of known relocations included within the core area (60–100%) were reported (Appendix Table A1).

Core areas and 95% UD (total home range) areas were extracted from R as shapefiles and projected in QGIS (QGIS Development Team, 2015). To evaluate how space was shared among female singing voles within a year, percent overlap of core areas was calculated by comparing the core area of each vole with the aggregate area of overlapping cores from the sample population. Trap stations were classified as either “shared” or “exclusive” based on whether they were included in the core area of multiple singing voles within a given year (“shared”; counted once per core area including this trap station) or in the core area of only one singing vole within a given year (“exclusive”). This definition of core area overlap identifies space used by multiple individuals but does not indicate whether that use co-occurred in time. Total encounters at “shared” trap stations and at “exclusive” trap stations within cores were divided by the total available trap stations within each category,

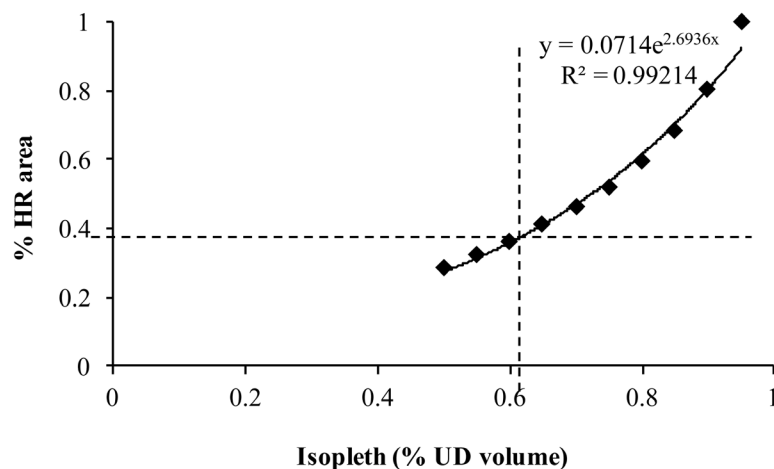


FIGURE 2. The utilization distribution (UD) isopleth delineating core area was calculated by determining where the first derivative of the curve equals 1. For this individual, the UD isopleth delineating core area was 61.2%, which represented 37.2% of the total home range area.

respectively, which yielded a standardized comparison of per-trap station use for each category in both 2013 and 2014. Considering use at the sample unit of a trap station facilitated the analysis of vole space use relative to habitat type and availability.

Microhabitat Affinity

The distribution of vole encounters across the 60 trap stations was analyzed using a linear regression to determine whether the frequency of use of a given trap station was consistent across years. To test for an impact of microhabitat affinity on space use, we analyzed encounters at each trap station relative to vegetation cover data both for individuals and at the population level. Multivariate hierarchical cluster analysis was used in program PC-ORD (McCune and Mefford, 2011) to identify a natural grouping structure of trap stations by similarity in vegetation cover composition, employing Sørensen distance measure and flexible beta linkage ($b = -0.25$) method. To facilitate this analysis, the vegetation cover data were re-coded to the mid-point of each Daubenmire cover class, such that six possible values were used (2.5, 15, 37.5, 62.5, 85, and 97.5).

Across the sampled landscape, observed use (aggregate encounters) of each microhabitat was compared relative to its availability (number of trap stations characterized in a given microhabitat). Specifically, the use rate was calculated by dividing aggregate encounters across all trap stations within a microhabitat category by the number of trap stations categorized as that microhabitat. Chi-squared tests were used to compare the observed use of microhabitats to the expected use (proportional to availability) by singing voles within each year across all microhabitats and within each microhabitat across both years (Neu et al., 1974; Byers and Steinhorst, 1984; Brandt and Lambin, 2007).

RESULTS

Activity Patterns and Population Density Estimates

Singing voles were active on the rocky floodplain throughout the day, though they were most frequently captured at midnight checks (39% of all captures) and least frequently captured at midday and evening checks (each 17% of all captures).

Abundance estimates of singing voles from the Huggins closed-captures model increased from 10.45 to 25.09 ($\pm 0.71 - 2.07$ SE) and from 5.13 to 14.35 ($\pm 0.36 - 0.62$ SE) across the 2013 and 2014 breeding seasons, respectively. All count data and abundance estimates are

reported in Table A2. The effective sampling area was estimated as 0.56 ha and 0.57 ha in 2013 and 2014, respectively; these areas were used to calculate densities from the abundance estimates. Population density estimates ranged from a peak of 44.79 ha^{-1} (August 2013) to a trough of 8.96 ha^{-1} (June 2014). While population density within a sampling session (i.e., within a month) was on average 45 ± 4 SE % lower in 2014 than in 2013, the general trend of population density increasing from June to August was consistent between years.

Home Range Size and Overlap

Relocation data within a year were modeled to estimate home ranges (2013, $n = 7$ individuals; 2014, $n = 10$ individuals). Summary statistics on home range values for modeled individuals are provided in Table A1. Home range area (95% isopleth) did not significantly increase with number of relocations ($r^2 = 0.18$, $F = 3.33$, $p = 0.09$). A two-tailed t -test showed the average number of relocations used to estimate home ranges was not significantly different between 2013 and 2014 (two-sample $t_9 = 1.11$, $p = 0.30$). Average MCP area was not significantly different between 2013 and 2014 (two-sample $t_7 = 0.81$, $p = 0.44$). Using KDEs, home range size (95% isopleth) and core area (61% isopleth) were estimated from the UD for each vole (Fig. 3). Average core area was not significantly different between 2013 ($= 997 \text{ m}^2$) and 2014 ($= 856 \text{ m}^2$) (two-sample $t_8 = 0.26$, $p = 0.80$). Average proportion of home range as core (two-sample $t_{15} = -0.48$, $p = 0.64$) and average relative intensity of use within core areas (61% isopleth divided into proportion of home range delineated as core) (two-sample $t_{14} = 0.02$, $p = 0.98$) also were not significantly different between years. Average area of core shared with other modeled core areas was $394 \pm 111 \text{ m}^2$ SE in 2013 and $467 \pm 87 \text{ m}^2$ SE in 2014 (example shown in Fig. 4).

One individual was relocated in both 2013 ($n = 16$) and 2014 ($n = 10$) and its core areas from 2013 (406 m^2) and 2014 (658 m^2) overlapped by 139 m^2 . Two other females marked as juveniles in 2013 had home ranges modeled in 2014, and neither of their core areas included any of their respective relocation points from 2013.

Space Use

The distribution of encounters across trapping stations was not significantly correlated between years ($r^2 = 0.04$, $F = 2.54$, $p = 0.12$) (Fig. 5). Within the subpopulation of voles for which home ranges were modeled, combined core areas covered a similar amount of the grid in both years (46 trap stations in 2013, 48 trap stations in 2014). Use of “shared” and “exclusive” trap

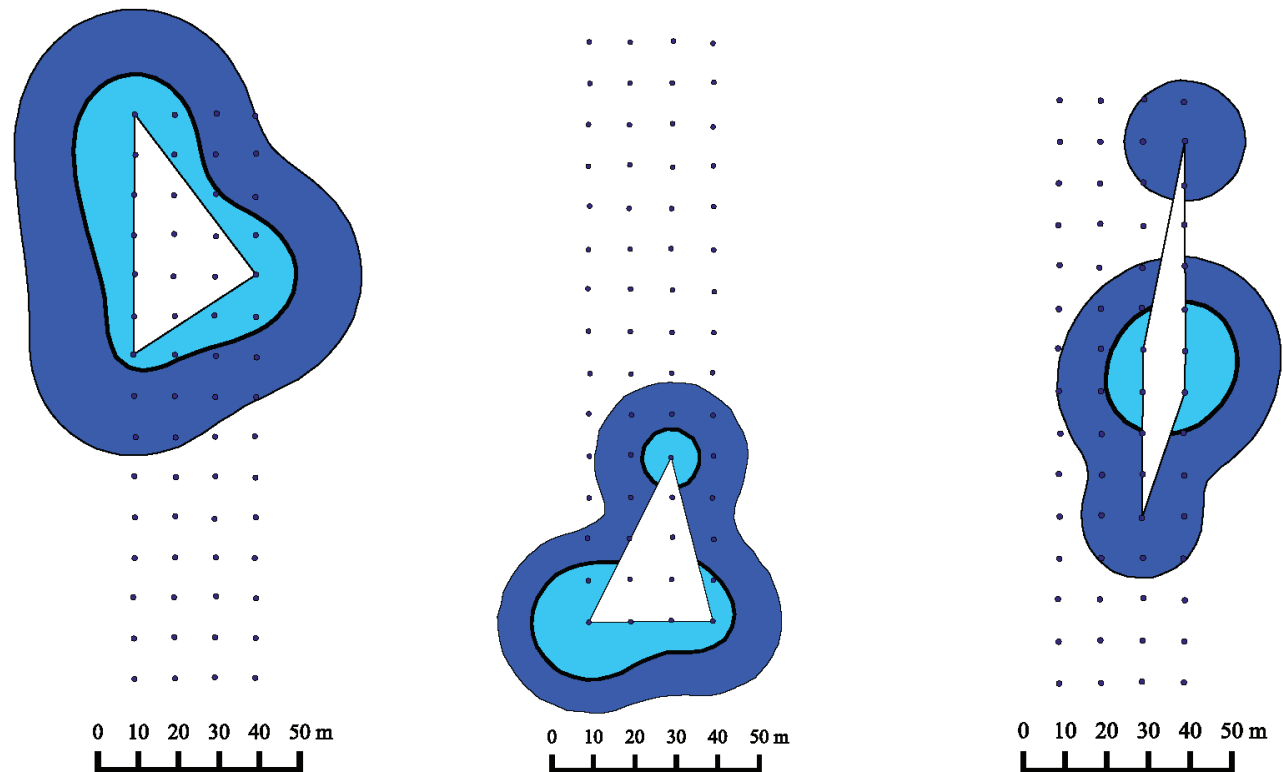


FIGURE 3. Representative models of home range (95% isopleth of the utilization distribution [UD], dark blue), core area (61% isopleth of the UD, light blue), and minimum convex polygon (MCP, white) for three female adult singing voles. The model on the left was constructed from 6 relocations; the model in the middle was constructed from 15 relocations; the model on the right was constructed from 14 relocations. Trap stations are overlaid for reference.

stations within core areas was assessed for both 2013 and 2014 (Table 1). Chi-squared tests showed that in 2013, use of “shared” trap stations was significantly greater than expected by proportional availability ($\chi^2 = 8.23$, $df = 1$, $n = 69$ encounters, $p < 0.01$), while in 2014, use of “shared” trap stations was not significantly greater than expected by proportional availability ($\chi^2 = 0.84$, $df = 1$, $n = 82$, $p = 0.36$).

Microhabitat Classification and Affinity

Hierarchical cluster analysis of vegetation cover data produced a dendrogram (Fig. A1) that was trimmed at six groups of trap stations (53% information remaining). Two sister groups, each with only four and two trap stations, respectively, were combined (at 47% information remaining) to meet minimum requirements for statistical tests. Each of the resulting five microhabitats had from 5 to 21 trap stations. Dominant or co-dominant cover types were used as labels for microhabitats (Fig. 6), based on average vegetation cover composition of all trap stations in that microhabitat (Fig. A2). The microhabitats were distinct, as exhibited by the long stems

separating most groups on the dendrogram, and separated along a gradient of bare rock cover (Fig. A2).

Use of microhabitats at the population level was assessed for both years (Table 2). In 2013 microhabitats were used disproportionately to their availability ($\chi^2 = 55.50$, $df = 4$, $n = 132$ encounters, $p < 0.001$), while in 2014 microhabitats were used marginally disproportionately to their availability ($\chi^2 = 31.99$, $df = 4$, $n = 120$, $p = 0.052$). Two microhabitat categories—EVEN and EQUISETUM—were used as expected based on availability across years. The remaining three categories were used differently than expected: BARE was used less than expected ($\chi^2 = 4.47$, $df = 1$, $n = 39$, $p = 0.035$), BARE + OTHER was used more than expected ($\chi^2 = 14.76$, $df = 1$, $n = 41$, $p < 0.001$), and SHRUB was used inconsistently between years ($\chi^2 = 6.72$, $df = 1$, $n = 70$, $p < 0.01$).

Use of microhabitats by individuals within their core areas was assessed for both 2013 and 2014 (Table 3). Chi-squared tests showed that in 2013 the use of trap stations by microhabitat category within combined core areas ($n = 7$) was disproportionate to the availability of microhabitats ($\chi^2 = 11.44$, $df = 4$, $n = 69$ encounters, p

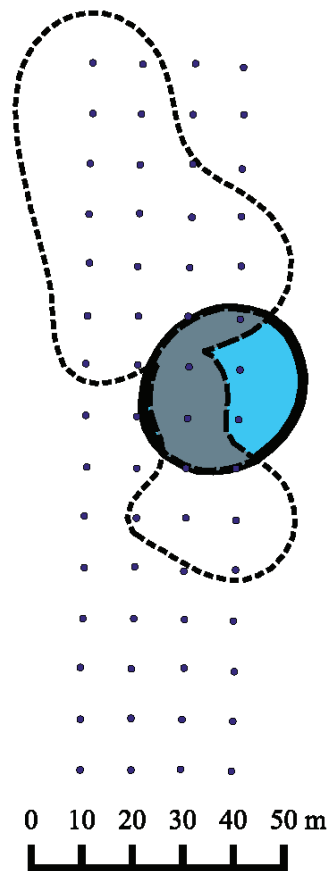


FIGURE 4. Model of exclusive and shared space of one adult female singing vole (solid thick border) (core area: 786 m²). Exclusive core space of this individual is shown in light blue (351 m², 45% of core area); space it shares with the core areas of two other female singing voles is shown in dark blue (435 m², 55% of core area). The core areas of those two individuals (one above, one below) are outlined with dashed borders. Trap stations are overlaid for reference.

= 0.02), while in 2014 the overall use of trap stations by microhabitat category within combined core areas ($n = 10$) was not disproportionate to their availability ($\chi^2 = 2.50$, $df = 4$, $n = 82$, $p = 0.64$).

DISCUSSION

Population Density and Activity Patterns

Population density estimates of singing voles were within the range (0–50 ha⁻¹) reported previously for this area (Batzli and Henttonen, 1993) and elsewhere (reviewed in Cole and Wilson, 2010). The interannual fluctuation observed (ca. 45% decline in density) was not atypical for rodent populations, especially microtine rodents at northern latitudes that undergo periodic high amplitude cycles in density (reviewed in Korpimäki et

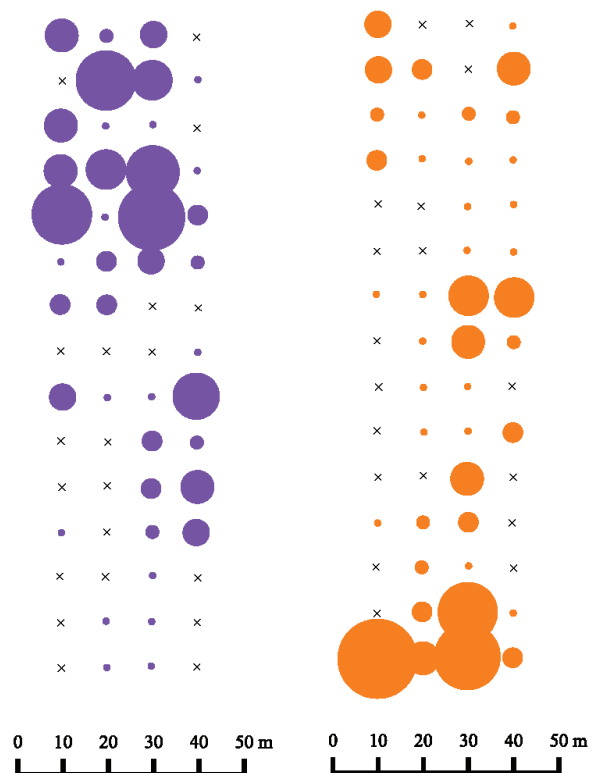


FIGURE 5. Distribution of singing vole encounters by trap station on the RF in 2013 (left panel, 132 aggregate encounters) and in 2014 (right panel, 120 aggregate encounters). Size of each circle corresponds to number of encounters at a trap station, ranging from 1 to 12. Xs represent trap stations with zero encounters. Encounters by trap station ($n = 60$) were not significantly correlated between 2013 and 2014 ($r^2 = 0.04$, $F = 2.54$, $p = 0.12$).

TABLE 1

Shared versus exclusive use of trap stations within core areas by singing voles on the rocky floodplain grid (RF). Available trap stations, observed encounters, and expected encounters are provided for each year. Use versus proportional availability was evaluated with a chi-squared test.

	Exclusive	Shared
2013 ($n = 7$ voles)*		
Trap stations	36	25
Observed encounters	29	40
Expected encounters	40.72	28.28
2014 ($n = 10$ voles)		
Trap stations	28	46
Observed encounters	27	55
Expected encounters	31.03	50.97

*Indicates significant difference from expected values (at $p < 0.05$).

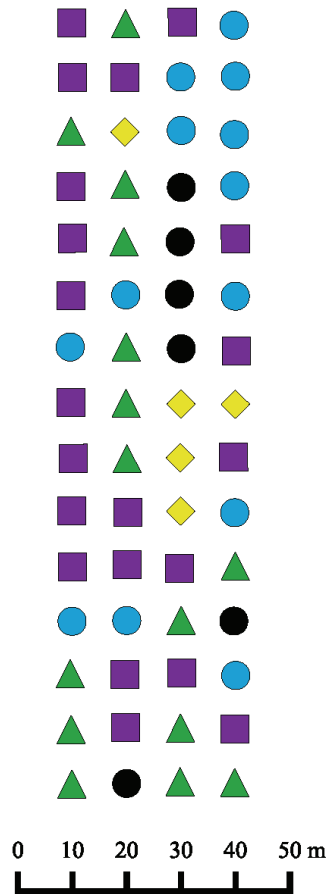


FIGURE 6. Trap stations on the RF coded by microhabitat: EVEN (purple squares, $n = 21$), SHRUB (green triangles, $n = 15$), BARE (blue circles, $n = 13$), BARE + OTHER (black circles, $n = 6$), and EQUISETUM (yellow diamonds, $n = 5$).

al., 2004). This population decline occurred over the winter and may reflect instability in the subnivean layer (Bilodeau et al., 2013; Duchesne et al., 2011; Korslund and Steen, 2006). In contrast, the population density decline observed (79%) at this site in the 1980s (Batzli and Henttonen, 1993) occurred over the course of a summer and resulted in density estimates (3.9 ha^{-1}) lower than those documented during the modern period (8.96 ha^{-1}).

Stability in Home Range Dynamics

Despite a ca. 45% decline in population density, average core area size, average proportion of home range as core area, and average intensity of use in core areas were consistent between 2013 and 2014. Mean home range size calculated using KDEs at the 95% isopleth of the UD and mean core area size from KDE at 61% UD decreased by only 15% and 14%, respectively, between 2013 and 2014. Moreover, core area contained on aver-

age 74% and 85% of known relocations in 2013 and 2014, respectively (Table A1).

Comparison of home range size today with data collected in the 1980s requires use of MCPs. MCP size of female adult and subadult singing voles reported by Batzli and Henttonen (1993) were similar to those reported here ($366\text{--}775 \text{ m}^2$ in 1984–1987 [$n = 28$], and $345\text{--}595 \text{ m}^2$ in 2013–2014 [$n = 17$]). MCPs underestimated home range areas compared to kernel KDE. Additionally, variance in MCP area between years was substantially greater than KDE area. MCP size decreased by 42% from 2013 to 2014. Comparisons between MCP and KDE core area models for the same individual displayed how MCP models may be skewed by outlier relocations, as opposed to KDE core area models. The repeatability of KDE under the parameters used in this study coupled with the objective verification of the core area as an area of intense use relative to the periphery allow these data to be comparable across studies, both for singing voles at alternate sites or for other microtine rodents.

These findings suggest that singing vole core area dynamics were not impacted by population density and support earlier findings by Batzli and Henttonen (1993). Galindo and Krebs (1985) suggested that as population density of a species in a given habitat increases, the suitability of that habitat decreases, assuming resources are limited. However, analysis of space use and microhabitat affinity by this population of singing voles did not indicate that habitat suitability was related to density, as assessed by interannual changes, suggesting habitat resources may not be limiting on the rocky floodplain.

Space Use

In a study of microtine space use, Douglass (1976) proposed that the balance of habitat preference and social interactions influencing an animal's space use changes along a gradient of habitat heterogeneity: at one end where habitats are sharply defined, habitat affinity is found to strongly drive space use; at the other end where habitats are more uniform, behavior plays a more predominant role in structuring space use. On the rocky floodplain, microhabitats were distinct and sharply defined (Fig. A1), albeit patchily distributed (Fig. 6), which suggests that microhabitat affinity may drive space use by the singing vole. Our findings indicate that not all core areas were continuous, which suggests that individuals exhibited patchy, concentrated activity within their home ranges (Fig. 3). We also observed a high degree of overlap given average core area size (40–55%; Table A1) in both years, suggesting that intraspecific interactions are also important in structuring space use for this social species.

TABLE 2

Population level microhabitat use by singing voles on the RF. Available trap stations, observed encounters, and expected encounters are provided for each year. Use versus proportional availability was evaluated with a chi-squared test.

	EVEN	SHRUB*	BARE*	BARE + OTHER*	EQUISETUM
Trap stations	21	15	13	6	5
2013 (<i>n</i> = 35 voles)*					
Observed encounters	52	27	20	27	6
Expected encounters	46.20	33.00	28.60	13.20	11.00
2014 (<i>n</i> = 17 voles)					
Observed encounters	34	43	19	14	10
Expected encounters	42.00	30.00	26.00	12.00	10.00

*Indicates significant difference from expected values (at $p < 0.05$).

TABLE 3

Microhabitat use within core areas aggregated for individual singing voles on the RF. Available trap stations, observed encounters, and expected encounters are provided for each year. Use versus proportional availability was evaluated with a chi-squared test.

	EVEN	SHRUB	BARE	BARE + OTHER	EQUISETUM
2013 (<i>n</i> = 7 voles)*					
Trap stations	17	11	7	6	5
Observed encounters	25	18	9	16	1
Expected encounters	25.50	16.50	10.50	9.00	7.50
2014 (<i>n</i> = 10 voles)					
Trap stations	15	12	11	5	5
Observed encounters	30	23	16	7	6
Expected encounters	25.63	20.50	18.79	8.54	8.54

*Indicates significant difference from expected values (at $p < 0.05$).

In 2013, space use by individuals was significantly impacted by both microhabitat affinity and intersection with core areas of other individuals, though neither factor was significant in 2014. Concentrated space use by multiple individuals and cooperative resource acquisition (e.g., haypiles built by multiple individuals) exhibited by singing voles (Batzli and Henttonen, 1993) may aid persistence under winter conditions through maintenance of subnivean space, which improves access to food caches, as documented among root voles during high-density winters (Hoset et al., 2009).

The interactive effects of social behavior and space use have implications for addressing the impact of

singing vole populations on tundra plant community composition. Shared space use elevates localized impacts including foraging, deposition of wastes (feces and urine), and cooperatively built haypiles and winter nests (Batzli and Henttonen, 1993). Such impacts can influence plant community composition, productivity, and overall biomass as well as nutrient cycling as exhibited in exclosure studies in this study system (Gough et al., 2007, 2012). Intense and localized effects of concentrated singing vole activity may reflect a pulse disturbance regime to the plant community, as observed through interannual shifts in space use at a population level (Fig. 5).

Microhabitat Affinity

The vegetation sampling indicated that the rocky floodplain was a mosaic of microhabitats for which singing voles exhibited significant affinities. This is in contrast to other tundra habitat types of the northern foothills of the Brooks Range, which show higher levels of homogeneity (Maguire, 2015). Composition of both the rocky floodplain overall and the combined core areas in terms of microhabitat types was similar, suggesting that the distribution (i.e., patchiness) of microhabitats across the grid is such that individual voles have access to a variety of microhabitats. The inclusion of bare cover (mostly exposed rock) across all microhabitat types, even as a nondominant cover type for many trap stations, suggests that the boulders on this habitat provide a critical structural refuge. The absence of visible nesting sites on the rocky floodplain, both in this study (Maguire, 2015) and in the findings of Batzli and Henttonen (1990) may suggest singing voles nest under the rocks and boulders.

It is possible that the characterization of microhabitats using composition of vegetation cover masks the importance of access to bare rock. The microhabitat dominated by bare rock (BARE), was under-utilized in both years at both the population level and within the core area of individuals. However, the ubiquity of bare rock cover across the rocky floodplain suggests that bare rock is an important resource on a broad spatial scale, even if microhabitats with a greater proportion of vegetation cover were selected for at a local scale. Affinity for rock cover has been reported for another alpine microtine, the European snow vole (*Chionomys nivalis*) (Luque-Larena et al., 2002), which selected for scree slopes.

Batzli and Lesieutre (1991) argued that availability of high-quality food was more important in habitat selection than structural elements for microtine rodents on the North Slope. In particular, they documented through diet analysis and food trials that *Equisetum arvense* is a highly palatable and preferred food source of the singing vole (Batzli and Lesieutre, 1991, 1995; Batzli and Henttonen, 1993). Despite their expectations, Batzli and Lesieutre (1991) found a weak correlation between abundance of this plant and the singing vole. Findings reported here confirm a weak association between *Equisetum* spp. and space use by the singing vole. The EQUISETUM microhabitat type was under-utilized or used at the expected level, at both the population level and individual level, which may be in part due to limited structural cover associated with this habitat type. In comparison, the BARE + OTHER microhabitat type was on average 12% *Equisetum* spp. cover, ranking second after the EQUISETUM microhabitat type in that

regard, but consisted of 38% bare rock cover. This microhabitat was over-utilized in both years at the population level as well as in 2013 at the individual core area level (BARE + OTHER was slightly under-utilized in 2014 at the individual core area level). The affinity for the BARE + OTHER microhabitat type indicates the importance of both vegetation (for food and cover) and bare rock (for cover or nesting sites) at a local scale.

The heterogeneity in available microhabitats on the rocky floodplain and the observed patterns of space use by the singing vole suggest that this habitat may promote resilience of this species to landscape-scale extrinsic pressures (e.g., poor winter weather and snow conditions that may limit access to winter food sources and decrease overwinter survivorship). This is supported by the findings of Duchesne et al. (2011) that heterogeneous microtopography and greater snow depth provide a more favorable microclimate for lemmings in northern Canada. In our study, heterogeneity in cover types across the rocky floodplain may have facilitated superior snowpack conditions for the singing vole population and reduced the decline in population density. The lack of heterogeneous microtopography on habitats occupied by the root vole may have diminished snowpack quality resulting in dampened population densities the following year (Maguire, 2015). Further measurement of habitat structure, microtopography, snowpack quality, and microclimate stability may facilitate more robust conclusions on the impact that the interaction of habitat features and stochastic winter weather events have on singing vole population dynamics in the northern foothills of the Brooks Range.

CONCLUSIONS

The findings presented here suggest both microhabitat affinity and social interaction (inferred through shared core areas) are important factors influencing singing vole space use at the population and individual core area level. The composition and patchy distribution of microhabitats across the rocky floodplain allows singing voles to access a variety of vegetation cover types, both within and among microhabitat categories. Concentrated singing vole activity, documented here through disproportionate use of shared trap stations within core areas, may substantially impact tundra plant communities through selective herbivory and nutrient deposition. Because use of individual trap stations across the grid was not consistent between years, the herbivore impacts on the tundra plant communities may represent a pulse rather than press disturbance regime. Further research addressing the interactive effects of social behavior, hab-

itat features, and diet on singing vole populations may clarify the dynamics of space use and their ecosystem impacts under a warming Arctic.

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REFERENCES CITED

- Andreassen, H. P., Hertzberg, K., and Ims, R. A., 1998: Space-use responses to habitat fragmentation and connectivity in the root vole *Microtus oeconomus*. *Ecology*, 79: 1223–1235, doi: <http://dx.doi.org/10.2307/176738>.
- Barg, J. J., Jones, J., and Robertson, R. J., 2005: Describing breeding territories of migratory passerines: suggestions for sampling, choice of estimator, and delineation of core areas. *Journal of Animal Ecology*, 74: 139–149, doi: <http://dx.doi.org/10.1111/j.1365-2656.2004.00906.x>.
- Batzli, G. O., and Henttonen, H., 1990: Demography and resource use by microtine rodents near Toolik Lake, Alaska, U.S.A. *Arctic and Alpine Research*, 22: 51–64.
- Batzli, G. O., and Henttonen, H., 1993: Home range and social organization of the singing vole (*Microtus miurus*). *Journal of Mammalogy*, 74: 868–878.
- Batzli, G. O., and Lesieutre, C., 1991: The influence of high quality food on habitat use by arctic microtine rodents. *Oikos*, 60: 299–306, doi: <http://dx.doi.org/10.2307/3545071>.
- Batzli, G. O., and Lesieutre, C., 1995: Community organization of arvicoline rodents in northern Alaska. *Oikos*, 72: 88–98.
- Bee, J. W., and Hall, E. R., 1956: Mammals of northern Alaska on the Arctic Slope. *Miscellaneous Publications of the Museum of Natural History University of Kansas*, 8: 1–309.
- Bilodeau, F., Gauthier, G., and Berteaux, D., 2013: The effect of snow cover on lemming population cycles in the Canadian High Arctic. *Oecologia*, 172: 1007–1016, doi: <http://dx.doi.org/10.1007/s00442-012-2549-8>.
- Brandt, M. J., and Lambin, X., 2007: Movement patterns of a specialist predator, the weasel *Mustela nivalis* exploiting asynchronous cyclic field vole *Microtus agrestis* populations. *Acta Theriologica* (Warsz), 52: 13–25, doi: <http://dx.doi.org/10.1007/BF03194195>.
- Byers, C. R., and Steinhorst, R. K., 1984: Clarification of a technique for analysis of utilization–availability data. *Journal of Wildlife Management*, 48: 1050–1053.
- Calenge, C., 2006: The package “adehabitat” for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling*, 197: 516–519, doi: <http://dx.doi.org/10.1016/j.ecolmodel.2006.03.017>.
- Cole, F. R., and Wilson, D. E., 2010: *Microtus miurus* (Rodentia: Cricetidae). *Mammalian Species*, 42: 75–89, doi: <http://dx.doi.org/10.1644/855.1>.
- Cooch, E. G., and White, G. C. (eds.), 2015: Program MARK: a Gentle Introduction, 14th ed.
- de Solla, S. R., Bonduriansky, R., and Brooks, R. J., 1999: Eliminating autocorrelation reduces biological relevance of home range estimates. *Journal of Animal Ecology*, 68: 221–234, doi: <http://dx.doi.org/10.1046/j.1365-2656.1999.00279.x>.
- Douglass, R. J., 1976: Spatial interactions and microhabitat selections of two locally sympatric voles, *Microtus montanus* and *Microtus pennsylvanicus*. *Ecology*, 57: 346–352.
- Duchesne, D., Gauthier, G., and Berteaux, D., 2011: Habitat selection, reproduction and predation of wintering lemmings in the Arctic. *Oecologia*, 167: 967–980, doi: <http://dx.doi.org/10.1007/s00442-011-2045-6>.
- Galindo, C., and Krebs, C. J., 1985: Habitat use by singing voles and tundra voles in the southern Yukon. *Oecologia*, 66: 430–436.
- Gough, L., Ramsey, E. A., and Johnson, D. R., 2007: Plant–herbivore interactions in Alaskan arctic tundra change with soil nutrient availability. *Oikos*, 116: 407–418, doi: <http://dx.doi.org/10.1111/j.2007.0030-1299.15449.x>.
- Gough, L., Moore, J. C., Shaver, G. R., Simpson, R. T., and Johnson, D. R., 2012: Above- and belowground responses of arctic tundra ecosystems to altered soil nutrients and mammalian herbivory. *Ecology*, 93: 1683–1694.
- Hoset, K. S., Le Galliard, J. F., Gundersen, G., and Steen, H., 2008: Home range size and overlap in female root voles: effects of season and density. *Behavioral Ecology*, 19: 139–145, doi: <http://dx.doi.org/10.1093/beheco/arm112>.
- Hoset, K. S., Le Galliard, J. F., and Gundersen, G., 2009: Demographic responses to a mild winter in enclosed vole populations. *Population Ecology*, 51: 279–288, doi: <http://dx.doi.org/10.1007/s10144-008-0130-4>.
- Hovland, N., Andreassen, H. P., and Ims, R. A., 1999: Foraging behaviour of the root vole *Microtus oeconomus* in fragmented habitats. *Oecologia*, 121: 236–244, doi: <http://dx.doi.org/10.1007/s004420050925>.
- Huggins, R. M., 1989: On the statistical analysis of capture–recapture experiments. *Biometrika*, 76: 133–140.
- Korpimäki, E., Brown, P. R., Jacob, J., and Pech, R. P., 2004: The puzzles of population cycles and outbreaks of small mammals solved? *Bioscience*, 54: 1071–1079, doi: [http://dx.doi.org/10.1641/0006-3568\(2004\)054\[1071:TPOPCA\]2.0.CO;2](http://dx.doi.org/10.1641/0006-3568(2004)054[1071:TPOPCA]2.0.CO;2).

- Korslund, L., and Steen, H., 2006: Small rodent winter survival: snow conditions limit access to food resources. *Journal of Animal Ecology*, 75: 156–166, doi: <http://dx.doi.org/10.1111/j.1365-2656.2005.01031.x>.
- Krebs, C. J., 2013: *Population Fluctuations in Rodents*. Chicago: University of Chicago Press.
- Krebs, C. J., Boonstra, R., Gilbert, S., Reid, D., Kenney, A. J., and Hofer, E. J., 2011: Density estimation for small mammals from livetrapping grids: rodents in northern Canada. *Journal of Mammalogy*, 92: 974–981, doi: <http://dx.doi.org/10.1644/10-MAMM-A-313.1>.
- Luque-Larena, J. J., López, P., and Gosálbez, J., 2002: Microhabitat use by the snow vole *Chionomys nivalis* in alpine environments reflects rock-dwelling preferences. *Canadian Journal of Zoology*, 80: 36–41, doi: <http://dx.doi.org/10.1139/z01-197>.
- Maguire, A. J., 2015: *Space Use and Habitat Affinities of the Singing Vole on the Northern Foothills of the Brooks Range, Alaska*. MS thesis, Department of Natural Resources and Environment, University of New Hampshire, Durham, 77 pp.
- McCune, B., and Mefford, M. J., 2011: PC-ORD. Multivariate Analysis of Ecological Data. Version 6. MjM Software, Gleneden Beach, Oregon, U.S.A.
- Myllymäki, A., 1977: Intraspecific competition and home range dynamics in the field vole *Microtus agrestis*. *Oikos*, 29: 553–569, doi: <http://dx.doi.org/10.2307/3543594>.
- Neu, C. W., Byers, C. R., and Peek, J. M., 1974: A technique for analysis of habitat utilization-availability data. *Journal of Wildlife Management*, 38: 541–545.
- Otis, D. L., Burnham, K. P., White, G. C., and Anderson, D. R., 1978: Statistical inference from capture data on closed animal populations. *Wildlife Monographs*, 62: 3–135.
- QGIS Development Team, 2015: QGIS Geographic Information System. Open Source Geospatial Foundation Project, <http://qgis.org/en/site>.
- R Core Team, 2015: *R: a Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Samuel, M. D., Pierce, D. J., and Garton, E. O., 1985: Identifying areas of concentrated use within the home range. *Journal of Animal Ecology*, 54: 711–719, doi: <http://dx.doi.org/10.2307/4373>.
- Seaman, D. E., and Powell, R. A., 1996: An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology*, 77: 2075–2085, doi: <http://dx.doi.org/10.2307/2265701>.
- Sikes, R. S., Gannon, W. L., and the Animal Care and Use Committee of the American Society of Mammalogists, 2011: Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy*, 92: 235–253, doi: <http://dx.doi.org/10.1644/10-MAMM-F-355.1>.
- Silverman, B. W., 1986: *Density Estimation for Statistics and Data Analysis Citation Information*. London: Chapman and Hall.
- Swingland, I. R., and Greenwood, P. J. (eds.), 1983: *The Ecology of Animal Movement*. Oxford: Oxford University Press.
- Van Winkle, W., 1975: Comparison of several probabilistic home-range models. *Journal of Wildlife Management*, 39: 118–123, doi: <http://dx.doi.org/10.2307/3800474>.
- Vander Wal, E., and Rodgers, A. R., 2012: An individual-based quantitative approach for delineating core areas of animal space use. *Ecological Modelling*, 224: 48–53, doi: <http://dx.doi.org/10.1016/j.ecolmodel.2011.10.006>.

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APPENDIX

Table A1

Summary statistics on home range analyses for female subadult and adult singing voles on the rocky floodplain. Only individuals captured ³ five times in a summer were included. Estimates are provided for the entirety of the home range (encompassed by the 95% isopleth of the utilization distribution), the core area (encompassed by the 61% isopleth of the utilization distribution), and the minimum convex polygon (using only known relocation coordinates). Additionally, proportion of relocations in the core area and core area shared other modeled core areas are included.

	Mean	S.E.	Minimum	Maximum
2013 (<i>n</i> = 7)				
# Encounters	11.43	2.14	5	18
# Unique relocation points	7	1.4	3	13
MCP area [m ²]	595	295	52	2290
Total HR area (95% UD) [m ²]	3031	1495	531	11,897
Core area (61% UD) [m ²]	997	496	164	3931
Proportion home range as core area	0.32	0.01	0.28	0.38
Proportion relocations in core area	0.74	0.05	0.6	1
Relative intensity of use	1.88	0.06	1.6	2.13
Area of overlap [m ²]	394	111	0.31	846
2014 (<i>n</i> = 10)				
# Encounters	8.8	1.04	6	15
# Unique relocation points	5	0.26	4	6
MCP area [m ²]	346	86	6	905
Total HR area (95% UD) [m ²]	2588	575	852	6892
Core area (61% UD) [m ²]	856	211	297	2560
Proportion home range as core area	0.33	0.01	0.22	0.39
Proportion relocations in core area	0.89	0.04	0.67	1
Relative intensity of use	1.88	0.11	1.55	2.76
Area of overlap [m ²]	467	87	95	943

Table A2

Counts and abundance estimates from a Huggins closed-capture model of singing voles on the rocky floodplain from each sampling session in 2013 and 2014.

		Abundance Estimate			
	Count	Mean estimate	Standard error	95% confidence interval (lower limit)	95% confidence interval (upper limit)
2013					
June	10	10.45	0.71	10.05	14.01
July	17	19.39	1.78	17.65	25.81
August	22	25.09	2.07	22.94	32.21
2014					
June	5	5.13	0.36	5.01	7.36
July	12	12.3	0.57	12.03	15.41
August	14	14.35	0.62	14.03	17.64

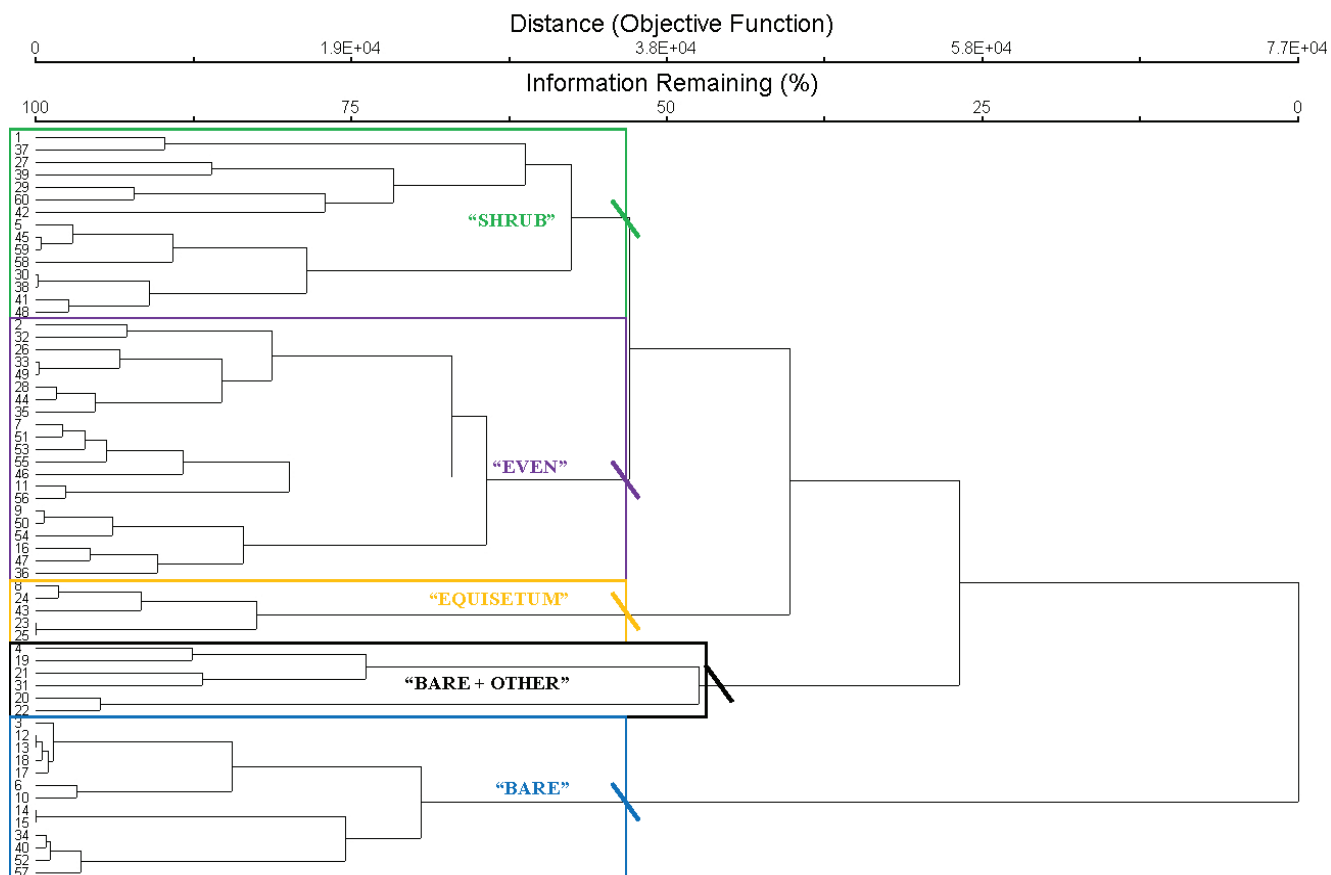


Figure A1. Dendrogram from hierarchical cluster analysis of vegetation cover composition of trap stations on the rocky floodplain grid. The dendrogram was initially cut at 53% information remaining. Two groups were then joined at 47% information. Microhabitats are labeled by the dominant cover type of the average composition of the trap stations (Appendix Fig. A2).

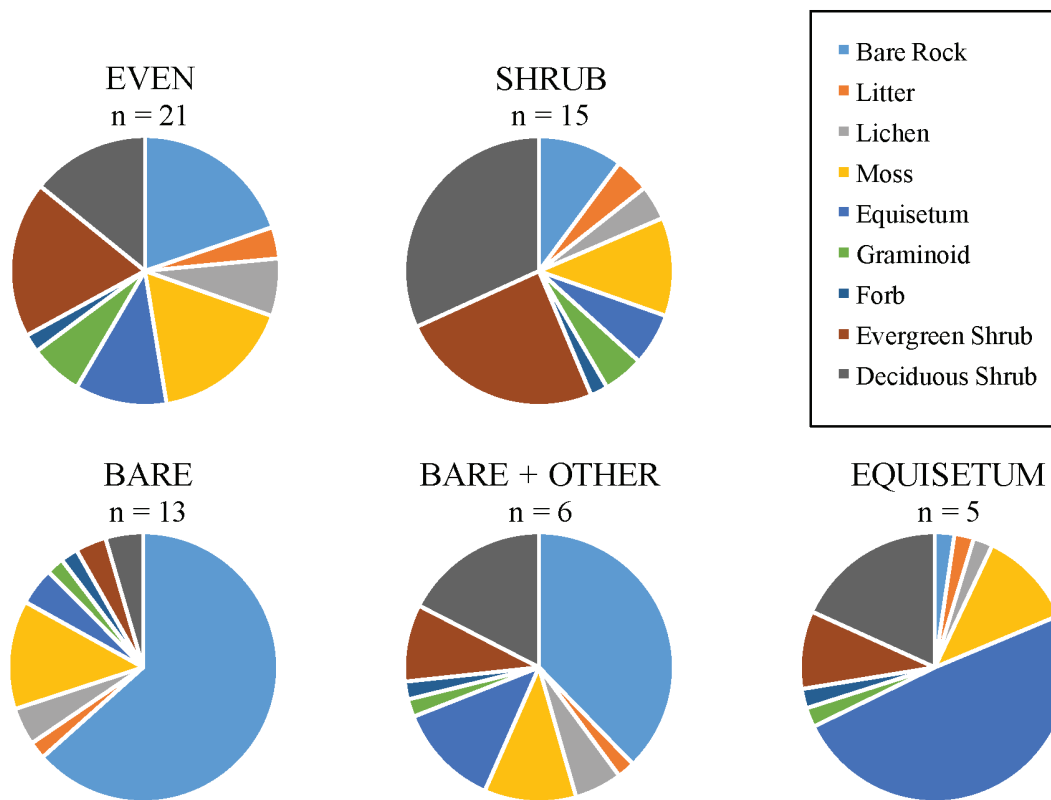


Figure A2. Mean vegetation cover composition of trap stations in each microhabitat category from nine cover types.