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# Space use and habitat affinities of the singing vole on the northern foothills of the Brooks Range, Alaska

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SPACE USE AND HABITAT AFFINITIES OF THE SINGING VOLE ON THE NORTHERN  
FOOTHILLS OF THE BROOKS RANGE, ALASKA

BY

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THESIS

Submitted to the University of New Hampshire  
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## ABSTRACT

### SPACE USE AND HABITAT AFFINITIES OF THE SINGING VOLE ON THE NORTHERN FOOTHILLS OF THE BROOKS RANGE, ALASKA

by

Andrew John Maguire

University of New Hampshire, December, 2015

Arctic tundra is being affected by a rapidly warming climate, which is accompanied by shifts in plant community composition and structure. Shrub expansion, a predominant consequence of this warming, is linked with changes in nutrient cycling and has direct implications to global change biology. Habitats are being altered across the landscape, with subsequent changes to arctic faunal communities. While herbivory has been noted as important in contributing to plant community composition in the arctic, with the potential to both exacerbate and mitigate shifts toward shrub-dominated tundra landscapes, little research has been conducted on herbivore dynamics. Microtine rodents (i.e., voles and lemmings) are the dominant vertebrate herbivores in the Alaskan Arctic. Through mark-recapture surveys and analysis of individual and population-level space use, I studied the population ecology of the microtine community to better establish the role of these small mammals in this rapidly changing region. Co-dominant species, the singing vole and the tundra vole, exhibit limited ecological overlap, preferring different habitat types and food sources. Results from surveys confirmed previously documented spatial segregation of the two co-dominant species by habitat along a moisture gradient. Interpretation of results suggest that extrinsic factors, possibly relating to stochastic winter climatic events, impact these co-dominant species differently. Over the duration of the

study, the singing vole was locally more abundant despite preferring regionally less available habitat, which suggests that its habitat may buffer singing vole populations from the affects of stochastic events. Analysis of space use by the singing vole indicated that both intraspecific interaction and microhabitat affinities played a role in local scale space use, which, through selective herbivory and concentrated deposition of nutrients, has implications on its role in structuring tundra plant communities. Further research on these species over a longer duration will classify the impact of extrinsic factors on population dynamics and the impact of resource use on local and landscape level changes to the tundra ecosystem.

## INTRODUCTION

### *Background*

The Alaskan North Slope is an ecologically unique region north of the tree line, characterized by continuous permafrost and limited nutrient availability. Under recent climate change, arctic regions have been warming at a rate two to three times higher than the global average (Anisimov et al. 2007), triggering marked changes to ecosystem structure and function (Hinzman et al. 2005, Wookey et al. 2009). Circumpolar warming is associated with an increased active layer for plant growth accompanied by compositional and structural shifts in plant communities across the tundra, most notably shrub expansion (Hinzman et al. 2005, Wookey et al. 2009, Post et al. 2009, Myers-Smith et al. 2011, Gough et al. 2012). Research has documented an encroachment of tall shrub species across the Arctic, which may mitigate or exacerbate local warming through feedbacks altering snow depth and albedo (Myers-Smith et al. 2011). While numerous studies have focused on contemporary changes in biogeochemistry, oceanography, glaciology, and climatology in the Arctic, with subsequent impacts on nutrient cycling and energy balance (reviewed in Hinzman et al. 2005), the influence of such systemic changes to habitat structure on terrestrial fauna and on their interactions with changing habitats have yet to receive comprehensive investigation.

Climate change can both directly and indirectly affect the distribution and abundance of fauna. A changing climate impacts faunal species distribution and abundance directly through physiological tolerance of abiotic conditions, and indirectly through timing of resource availability among habitats (Hinzman et al. 2005), creating potential mismatches between



species and their resources. Furthermore, in arctic regions climate change may reduce or increase both habitat suitability and availability (Hinzman et al. 2005). Particularly in river valleys of the Brooks Range and North Slope uplands, the transition from grassland tundra to tall, canopy-forming deciduous shrub cover is expected to have dramatic implications for arctic ecosystem processes (Naito and Cairns 2014). This change in vegetation structure will impact the availability of habitat for resident small mammal herbivores, and may influence species occurrence and abundance.

Climate governs the structure of the plant communities across the North Slope, whereas the heterogeneity of plant communities at a landscape level is linked to topography, substrate, aspect (Huryh and Hobbie 2012), soil and permafrost conditions, and snow regime (Naito and Cairns 2014). At the local scale, composition of plant communities is also heavily influenced by herbivores (Wookey et al. 2009). Differential resource use by vertebrate herbivores on the North Slope will therefore contribute to non-uniform responses of tundra plant communities to changing climatic conditions (Hinzman et al. 2005), potentially altering ecosystem function at a landscape scale (Myers-Smith et al. 2011). In order to better understand the consequences of climate change in the Arctic, herbivores must be adequately incorporated in broader research endeavors.

Plant-herbivore interactions have been well-studied in tallgrass prairies. This research suggests that meadow voles (*Microtus pennsylvanicus*) create consistent effects on plant abundance, similar in scale to their ungulate counterparts, yet with distinct effects on the composition of those plant communities (Howe et al. 2006). Moreover, exclosure studies demonstrate that small mammal herbivores in Arctic Alaska impact both the composition and structure of tundra plant communities through selective foraging (McKendrick et al. 1980,

Gough et al. 2007, 2012). Furthermore, studies have shown that the abundance of small mammal herbivores drives the population dynamics of predators (Pitelka et al. 1955, Batzli and Lesieutre 1995, Korpimäki et al. 2002, Gough et al. 2012). Research on such impacts across trophic levels is acutely important where small mammals are the dominant resident herbivores, as in the Alaskan Arctic tundra.

In light of the mosaic of distinct plant communities in the Arctic (Huryh and Hobbie 2012), understanding the impact of small mammal herbivory is important at local- and landscape-scales. Evidence from across the circumpolar region has documented herbivore impacts both in patch-scale plant community structure (Grellmann 2002, Gough et al. 2007, 2012, Olofsson et al. 2009, Johnson et al. 2011) and landscape-scale (770 km<sup>2</sup>) reductions in normalized difference vegetation index (NDVI) following combined vole and lemming peak population years (Olofsson et al. 2004), detectable from satellite-derived (MODIS) images (Olofsson et al. 2012, 2013). Research on interactions between warming simulations (i.e., soil nutrient enrichment) and mammalian herbivory (i.e., herbivore-excluded and open plots) have suggested that herbivory can both exacerbate (Gough et al. 2012) and dampen (Olofsson et al. 2009) the transition of vegetation from graminoid to shrub-dominated tundra. However, the responses of such herbivores to resource dynamics under a changing arctic climate remain poorly documented (Gough et al. 2007, 2012, Díaz et al. 2007, Wookey et al. 2009), and are species-specific (Grellmann 2002).

Microtine rodents (subfamily Arvicolinae, e.g., voles and lemmings) are globally distributed herbivores often noted for exhibiting regular (3-5 year) cycles in population fluctuations (Batzli and Henttonen 1990, Korpimäki et al. 2002). Recent research in Scandinavia suggests that these cycles may be dampening in amplitude and periodicity as a consequence of

regional warming (Hörnfeldt et al. 2005, Ims et al. 2008, Kausrud et al. 2008, White 2011, Hansen et al. 2013). Research in Arctic Alaska on the ecology of microtine rodents and their population cycles has not occurred in over two decades (McKendrick et al. 1980, Batzli and Henttonen 1990, 1993, Batzli and Lesieutre 1991, 1995), a period marked by rapid warming (Myers-Smith et al. 2011, Gough et al. 2012).

Teasing apart the independent and interactive effects of changes in climate and herbivore pressure on structural and compositional shifts in tundra plant communities is necessary to fully comprehend the mechanisms of regional ecosystem responses. Establishing current demographic baselines and addressing basic questions on population ecology, space use, and the habitat affinities of these microtine rodents can facilitate investigations into the relationships between changes in climate, variance in plant community structure, and resource use by small mammal herbivores.

### *Overview of the study system*

Field research was conducted on the northern foothills of the Brooks Range in Alaska (68° 38' N, 149° 36' W at 720 m above sea level), located near Toolik Field Station. Whereas globally, vertebrate herbivores are a diverse functional group (Huntly 1991), the Arctic has few representative species. The prominent vertebrate herbivores in Arctic Alaska are transient herds of caribou (*Rangifer tarandus*) and resident microtine rodents. While caribou herds have substantial impacts on vegetation through grazing and trampling (McKendrick et al. 1980, Myers-Smith et al. 2011), they are migratory and not continuously (year-round) present within the foothills of the Brooks Range. Moose (*Alces americanus*) and snowshoe hares (*Lepus americanus*) occur in much lower densities and are restricted to willow thickets (Huryn and

Hobbie 2012). Arctic ground squirrels (*Urocitellus parryii*) are residential rodents, yet are omnivorous, display different behavioral patterns (hibernating for approximately half of the year), and are restricted to areas with a deep active layer (seasonally thawing soil) for constructing burrows (Huryin and Hobbie 2012). Shrews are regionally widespread but are non-rodent insectivorous small mammals.

Microtine rodents are small mammal herbivores that rapidly mature, have high reproductive potential, and exhibit short-term population turnover (i.e., short life expectancy) (Tamarin 1985). They are ubiquitous on the North Slope of Alaska, remaining active year-round, and are known to substantially affect tundra plant communities (McKendrick et al. 1980, Batzli and Lesieutre 1995, Olofsson et al. 2004, 2012, 2013, Gough et al. 2007, 2012). On the North Slope of Alaska, five resident microtine rodents occur: singing vole (*Microtus miurus*), tundra vole (*M. oeconomus*), northern red-backed vole (*Myodes rutilus*), collared lemming (*Dicrostonyx groenlandicus*), and brown lemming (*Lemmus trimucronatus*) (Bee and Hall 1956, Batzli and Henttonen 1990). However, only two of these species, the singing vole and the tundra vole are widespread and abundant on the northern foothills of the Brooks Range, and the co-dominance of these two species is unique to this region of Arctic Alaska (Batzli and Henttonen 1990, Batzli and Lesieutre 1991, 1995).

In this region, singing voles and tundra voles are abundant, yet with marked differences between species in distributions across a moisture gradient of habitat types (Batzli and Henttonen 1990, Batzli and Lesieutre 1995). Such spatial segregation has also been documented in subarctic regions (Galindo and Krebs 1985). Coupling distinct habitat affinities with high specificity in diet (the singing vole prefers *Equisetum arvensis*, *Vaccinium uliginosum*, and *Salix glauca* whereas the tundra vole prefers *Eriophorum angustifolium*) (Galindo and Krebs 1985, Batzli and

Henttonen 1990, 1993, Batzli and Lesieutre 1991, 1995, Turchin and Batzli 2001) creates an excellent framework for investigating resource use by herbivores on a rapidly changing landscape.

Tundra plant communities common to the region include: *rocky floodplain*, low habitat characterized by patches of soil and vegetation—dominated by a shrub canopy—on large rocks; *heath*, dry or mesic upland habitat characterized by low evergreen shrubs and lichen; *moist nonacidic tundra*, habitat characterized by non-tussock-forming sedges, dwarf shrubs, and non-sphagnum moss; *moist acidic tundra*, upland habitat characterized by tussock-forming and rhizomatous sedges, deciduous shrubs, evergreens, forbs, lichen, and sphagnum moss; *shrub tundra*, habitat dominated by a canopy of deciduous shrubs; and *wet swales* and *fens*, poorly drained lowland habitat characterized by rhizomatous sedges, scattered dwarf shrubs, and a moss mat (Batzli and Henttonen 1990, Gough 2006, Wookey et al. 2009). Representative areas of each these habitat types were surveyed during this study.

Prior work at this study site established that the singing vole and the tundra vole segregate spatially across habitats along a moisture gradient (*M. miurus* favoring mesic habitats and *M. oeconomus* favoring low, wet habitats) (Batzli and Henttonen 1990). Analysis of stomach contents and food trials have shown that these species prefer foods dominant in their respective habitats, which reduces ecological overlap of the two species at any given site (Batzli and Henttonen 1990, Batzli and Lesieutre 1991, 1995). However, limited research has been conducted on space use by these species at a local scale and on the impacts that microtine rodents may have on the rapidly changing Alaskan Arctic landscape.

### *Research objectives*

This research addresses fundamental facets of population ecology (demographics, space use, and habitat affinities) of microtine rodents across a gradient of tundra plant communities on the northern foothills of the Brooks Range, Alaska. Results inform understanding of the effects of changing plant communities on these dominant and ubiquitous herbivores, and the roles they play in structuring the broader arctic tundra ecosystem. Specific objectives are to:

1. Establish baseline demographic data over three consecutive breeding seasons (summers 2013 - 2015).
2. Quantify space use through mark-recapture live trapping.
3. Analyze habitat affinities through comparison of relocation data and associated vegetation composition.

### *Organization of thesis*

This report is written in two chapters, focusing on different elements of the study. The first chapter summarizes the demography of microtine rodents in the northern foothills of the Brooks Range, Alaska. Age structure, count data, and associations with six different tundra plant communities during the vegetation growing season of encountered microtine rodents are reported.

The second chapter focuses on one population of singing voles which was analyzed for patterns of space use and microhabitat affinities. Intensive surveys described in chapter 1 yielded a more extensive data set on this population than on others surveyed, allowing deeper analysis of local-scale space use. Population densities were estimated for each of three sampling sessions in two consecutive summers. Home range analysis was conducted to describe core areas of intense

use and to characterize shared and exclusive space use, integrating the influence of intraspecific interactions on overall space use by the population. Comparing vole activity with described microhabitats relative to their respective availability, both on the scale of the aggregate population and within core areas, reveals trends in microhabitat affinities.

## CHAPTER I

### DEMOGRAPHY OF VOLES NEAR TOOLIK LAKE, ALASKA

#### **Introduction**

Extensive research conducted on the northern foothills of the Brooks Range in Alaska has enhanced our understanding of the factors that control ecosystem structure and function in the arctic tundra, including experimental manipulation to predict effects of environmental change (Gough et al. 2007, 2012). In contrast, much less is known about the current distribution and abundance of vertebrate herbivores in this region, how they respond to environmental change, and how those impacts may influence ecosystem processes at local and landscape scales.

Intensive studies on the population dynamics and resource use of microtine rodents (subfamily Arvicolinae, e.g., voles and lemmings)—ubiquitous resident herbivores—have been limited to a period of sampling conducted in the mid 1980s (Batzli and Henttonen 1990, 1993, Batzli and Lesieutre 1991, 1995), prior to the onset of rapid warming. Experimental manipulations conducted across a range of arctic ecosystems have shown that while warming or fertilization alone can enhance above ground productivity and nutrient cycling, when coupled with the presence of mammalian herbivores—including microtine rodents—responses were variable (Grellmann 2002, Gough et al. 2007, 2012, Post and Pedersen 2008, Olofsson et al. 2009). These findings highlight the importance of incorporating microtine rodents into broader research on ecosystem processes and plant community composition.



The dominant microtine species in this region, the tundra vole (*Microtus oeconomus*) and the singing vole (*M. miurus*), express distinct habitat preferences and diets which are manifested in reduced spatial overlap and limited interspecific competition (Galindo and Krebs 1985, Batzli and Henttonen 1990, 1993, Batzli and Lesieutre 1991, 1995). A third vole species, the northern red-backed vole (*Myodes rutilus*) and two lemming species, the collared lemming (*Dicrostonyx groenlandicus*) and the brown lemming (*Lemmus trimucronatus*), are present but rare (Bee and Hall 1956, Batzli and Henttonen 1990). Present day surveys of the microtine community in this region are necessary to evaluate whether the findings of Batzli and Henttonen (1990) on habitat use and distribution still hold, to investigate space use, to establish a new baseline for population density for continued monitoring under climate change, and to facilitate interdisciplinary research on herbivore impacts on ecosystem function. While microtine populations in many arctic regions historically exhibit dramatic yet regular fluctuations in their population densities over time (Batzli and Henttonen 1990, Korpimäki et al. 2002), recent studies suggest that such cycling may be dampening as a consequence of climate change (Hörnfeldt et al. 2005, Ims et al. 2008, Kausrud et al. 2008, White 2011, Hansen et al. 2013).

The tundra (or root) vole is a Holarctic species, broadly distributed across northern Europe, Asia, and North America. Males are territorial during the breeding season (Lambin et al. 1992) and prefer wet sedge habitats (Galindo and Krebs 1985, Batzli and Henttonen 1990, Ale et al. 2011). The singing vole is a Nearctic species, distributed across Alaska to northwestern Canada (Cole and Wilson 2010). Its space use is influenced by both social interactions with a high degree of home range overlap and by an affinity for mesic (i.e., well-drained) habitats (Batzli and Henttonen 1990, 1993, Batzli and Lesieutre 1995).

Both species rely on the subnivean layer (the interface between soil and snow (Pauli et al. 2013)) in the winter (Korslund and Steen 2006, Duchesne et al. 2011, Bilodeau et al. 2013), which highlights the impact of a warming climate on the distribution and abundance of microtine populations by reducing winter survivorship through reduced snowpack quality. In addition, the top-down impact of predation strongly influences cycles of vole abundance (Turchin and Batzli 2001, Korpimäki et al. 2002). On the North Slope of Alaska, common mammalian and avian predators include weasels, foxes, jaegers, and owls (Bee and Hall 1956).

The relatively small home range sizes (Lambin et al. 1992, Batzli and Henttonen 1993) of the small-bodied tundra vole and the singing vole allow for high resolution analysis of space use along with the responses of these species to local heterogeneity in habitat. Similarly, the rapid changes in microtine population abundance (Batzli and Henttonen 1990, Korpimäki et al. 2002) – resulting in part from short generation time and high fecundity – allow for the potential to study density-related impacts on space use and habitat affinities.

Here, I present results from intensive live trapping of the microtine community on a gradient of habitats on the northern foothills of the Brooks Range, Alaska near Toolik Field Station. The objective of this study was to document differences in demographic patterns and relative abundance between the two co-dominant species within and among habitat types in order to provide support for the hypothesis that extrinsic conditions drive these trends at a population level.

## Methods

### *Field surveys*

Surveys were conducted on the northern foothills of Alaska's Brooks Range (68° 38' N, 149° 36' W at 720 m above sea level) near Toolik Field Station (TFS). The design and placement of mark-recapture grids were based in part on previous microtine rodent sampling conducted by Batzli and colleagues in the 1980s at TFS (Batzli and Henttonen 1990, 1993, Batzli and Lesieutre 1995). Tundra plant communities were selected along a moisture gradient. In June 2013, four 0.42-ha grids were established, each in a distinct tundra community: rocky floodplain (RF), moist nonacidic tundra (MNT), moist acidic tundra (MAT13), and fen (FEN) (Figure 1.1). Each grid was 30m x 140m with 60 trap stations spaced 10m apart. Two Sherman live traps (H. B. Sherman, Tallahassee, Florida, USA) were baited with peanut butter and set to signs of vole activity (e.g., latrine, runway, grazed vegetation) within 2-m of each trap station, for a total of 120 traps per grid. Three discrete sampling sessions were conducted during the summer, in early June following snowmelt, in July about peak green-up, and in August during senescence. In each session, grids were sampled for four consecutive nights, with traps checked approximately every six hours (midnight, morning, midday, evening). Across the summer season each grid was surveyed for 1,440 trap-nights, with a total of 5,040 trap-checks.

In 2014 six grids were surveyed, including the RF, MNT, and FEN grids established in 2013. The representative moist acidic tundra grid was relocated due to low capture rates ( $n = 5$ ). Including this relocation, three additional grids were established: moist acidic tundra (MAT14) and shrub tundra (SHRUB) at Imnavait Creek, approximately 6.5 miles east of TFS, and mesic heath (MH) near the Kuparuk River, approximately 4.5 miles east of TFS (Figure 1.1). In 2015

the same six grids were surveyed in July only, each for 480 trap-nights, with a total of 1,680 trap-checks.

Upon capture each individual was identified to species, and sex, age (juvenile, sub-adult, adult), reproductive condition, and weight (using a Pesola® scale) were recorded. A Passively Integrated Transponder (PIT) tag was implanted in each individual at the first capture to allow for recognition upon successive captures. In addition, a small ear biopsy was taken on the initial capture along with a hair sample (cut from the dorsal hindquarters) and a fecal sample (from the trap), which were again collected on the initial capture of each successive trapping session in which an individual was caught. Incidental mortalities were retained and processed as voucher specimens and deposited at the University of Alaska Museum of the North.

Relative snow cover and flooding was noted at the trap-station level on each grid in June each summer. Grids were surveyed for presence of vole sign (e.g., winter nests, latrines, grazed) at trap-station level in June 2014 as a coarse assessment of over winter occupancy and abundance of voles. The vegetation at each trap station was characterized in July (during peak growing season) of the first survey year for each grid. Using a 1 m x 1 m quadrat at each trap station, cover was recorded using the Daubenmire scale (<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, deciduous shrub). Vegetation cover data were assumed to be representative of the area surrounding each trap station.

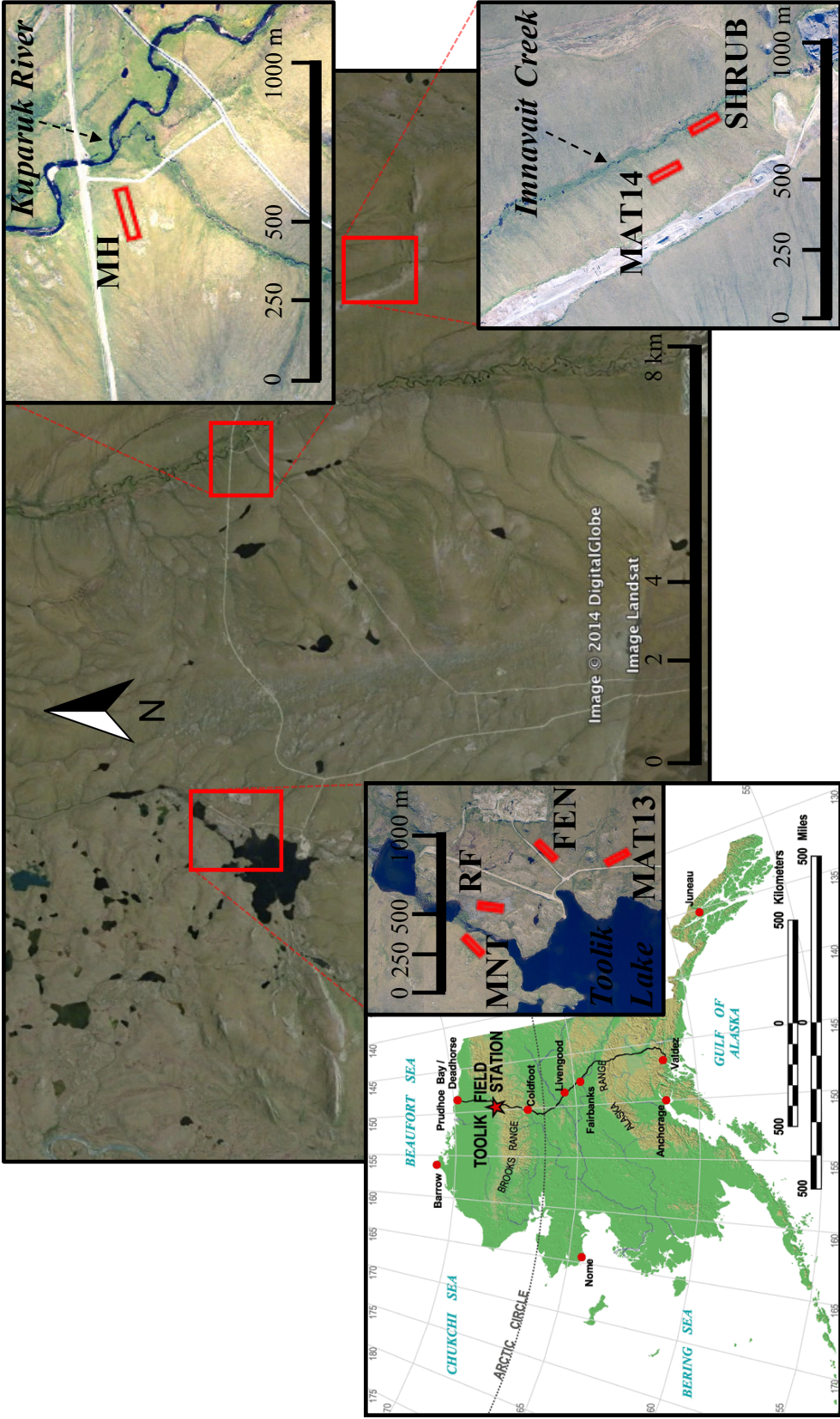


Figure 1.1. Toolik Lake study area with survey grids. Grids are labeled on inset maps by habitat type: *MNT*: moist nonacidic tussock tundra; *RF*: rocky floodplain; *FEN*: fen; *MAT13*: moist acidic tussock tundra; *MH*: mesic heath; *MAT14*: moist acidic tussock tundra; *SHRUB*: shrub tundra. Location of TFS in Alaska is indicated to the lower left (map provided by Toolik Field Station GIS Department).

## Results

### *Habitat composition*

Percent cover of vegetation by nine functional groups was compiled to differentiate between grids (Figure 1.2). The dominant cover type of the rocky floodplain grid (RF) was bare, which distinguished it from the other types. The moist nonacidic tundra grid (MNT), moist acidic tundra grids (MAT13 and MAT14), and fen (FEN) grid were each dominated by graminoids, namely *Eriophorum* spp. sedges. The mesic heath (MH) and shrub tundra grids (SHRUB) were superficially similar based on their dominant percent cover as moss followed by deciduous shrub; however, the shrub cover on MH was generally dwarf shrubs, and much more prostrate, while SHRUB was characterized by a canopy of erect *Betula nana* and *Salix* spp.

### *Abundance and encounters*

Over the course of the study (2013 – 2015) 156 unique individuals of three microtine species were captured (Table 1.1). Singing voles were the most abundant species in each year. Tundra voles were less abundant in 2013, though they were nearly as abundant as singing voles in 2014 ( $n = 24$  and  $n = 28$ , respectively). Northern red-backed voles were not captured in 2013, and ranked behind singing voles and tundra voles in abundance in both 2014 and 2015. Additionally, several non-target taxa were captured, though not marked. These included arctic ground squirrels (*Urocitellus parryii*) (2013: 15 encounters; 2014: one encounter), ermine (*Mustela ermina*) (2014: two encounters), and shrews (*Sorex* spp.) (2014: 10 encounters).

Surveys yielded 197 captures of 73 individual voles across four grids in 2013, 216 captures of 57 individual voles across six grids in 2014, and 66 captures of 30 individual voles across six grids in 2015 (July only). Aggregate encounters and rate of recaptures on RF were

substantially greater than on any of the other tundra habitats surveyed in 2013 through 2015 (Table 1.2). As such, this population was analyzed for home range dynamics and habitat affinities in Chapter 2.

In 2013, mean capture rate was 0.98% (based on trap-checks), ranging from 2.62% on RF – 0.24% on MAT. In 2014, mean capture rate was 0.71%, ranging from 2.38% on RF – 0.20% on MNT. In 2015, mean capture rate was 0.65%, ranging from 1.31% on RF – 0.06% on FEN.

Abundance of vole species differed by habitat type (Figure 1.3). Singing voles were more abundant on the mesic habitats, particularly at RF and MH, though one individual was caught at FEN on one occasion. In 2013, only singing voles occupied MNT; in 2014 and 2015, this habitat was occupied by both singing voles and tundra voles, with one northern red-backed vole appearing in 2015. Tundra voles were present on the wetter habitat types and most abundant at FEN. Northern red-backed voles were present on every habitat type except for MH, though in low abundances on each.

### *Demographics*

Age structure shifted toward a younger demographic across the summer season, for each species captured, with juveniles only captured in July and August. (Figure 1.4). Four individuals (of a total 73) initially captured in 2013 were recaptured in 2014 on the same (RF) grid. All were singing voles: three female and one male. Three were juveniles (one male, two female), initially captured in July or August of 2013, and were recaptured 4 – 15 times in 2014. The fourth was an adult female, initially captured in June 2013, and was recaptured 14 more times in 2013 (June, July, and August sampling sessions) and again 10 times in 2014 (July and August sampling

sessions). Weight progressions of these individuals were tracked to approximate growth patterns and change in body condition over winter (Figure 1.5).



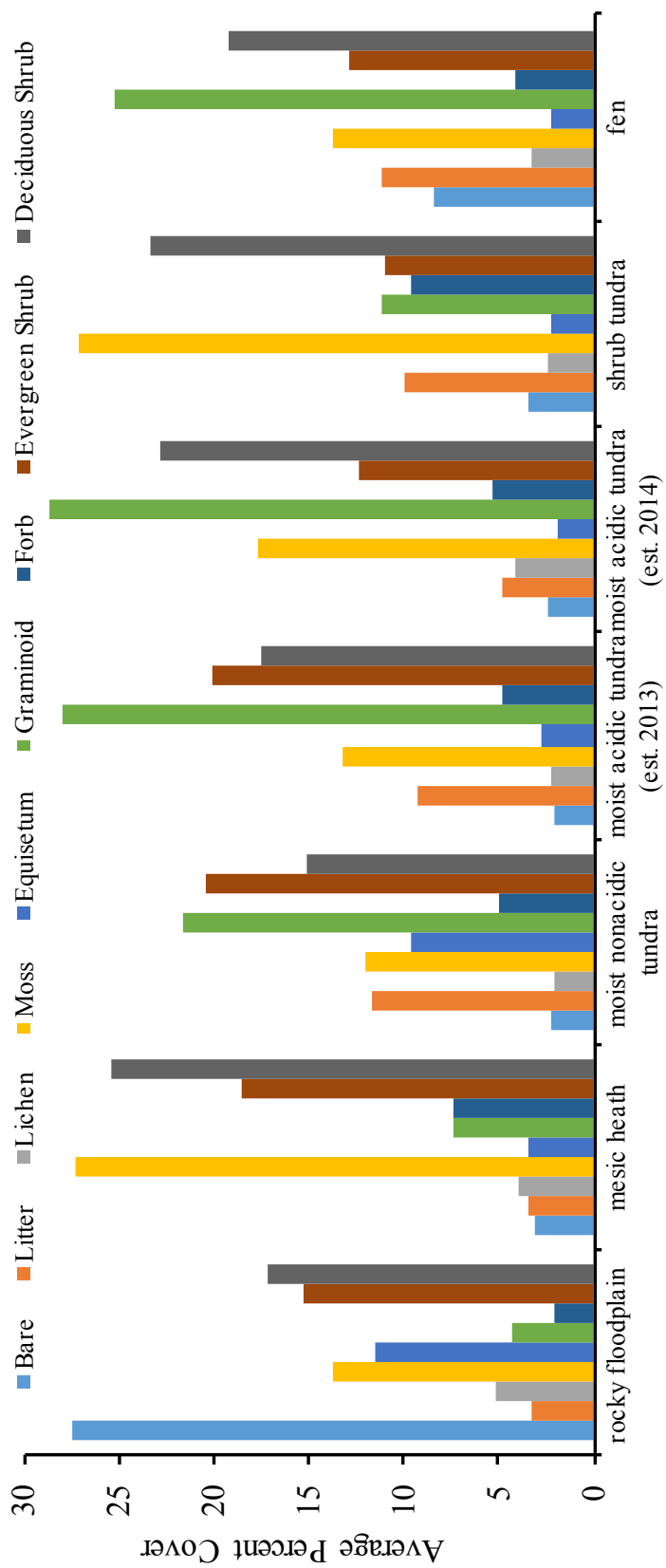


Figure 1.2. Average percent cover of nine vegetation functional groups from the 60 1 m<sup>2</sup> quadrats surveyed on each of the seven mark-recapture grids (arranged along a moisture gradient from well-drained to poorly-drained).

Table 1.1. Abundance of vole species in years surveyed on each grid (RF: rocky floodplain; MH: mesic heath; MNT: moist nonacidic tundra; MAT13: moist acidic tundra, est. 2013; MAT14: moist acidic tundra, est. 2014; SHRUB: shrub tundra; FEN: fen). Grids that were not surveyed in a given year were reported as “—” for each species. \*One northern red-backed vole was captured on both SHRUB and MAT14 in 2014, so totals for each grid reflect this, as does the total for all northern red-backed voles in 2014. \*\*Surveys in 2015 were conducted in July only, thus lower values reflect this difference in survey effort compared with 2013 and 2014.

	singing vole ( <i>Microtus miurus</i> )			tundra vole ( <i>Microtus oeconomus</i> )			northern red-backed vole ( <i>Myodes rutilus</i> )			TOTAL		
	2013	2014	2015**	2013	2014	2015**	2013	2014	2015**	2013	2014	2015**
RF	35	17	12	0	0	0	0	0	1	35	17	13
MH	—	8	2	—	0	0	—	0	0	—	8	2
MNT	12	2	4	0	3	1	0	0	1	12	5	6
MAT13	0	—	—	5	—	—	0	—	—	5	—	—
MAT14	—	0	0	—	3	4	—	1	0	—	4	4
SHRUB	—	0	0	—	5	4	—	1	0	—	6	4
FEN	0	1	0	21	13	1	0	4	0	21	18	1
TOTAL	47	28	18	26	24	10	0	5*	2	73	57	30

*Table 1.2. Aggregate encounters of all vole species in years surveyed at each grid (RF: rocky floodplain; MH: mesic heath; MNT: moist nonacidic tundra; MAT13: moist acidic tundra, est. 2013; MAT14: moist acidic tundra, est. 2014; SHRUB: shrub tundra; FEN: fen). Grids not surveyed in a given year are displayed as “—”. \*Surveys in 2015 were conducted in July only.*

	2013	2014	2015*
RF	132	120	22
MH	—	18	20
MNT	20	10	10
MAT13	12	—	—
MAT14	—	13	7
SHRUB	—	11	6
FEN	34	44	1

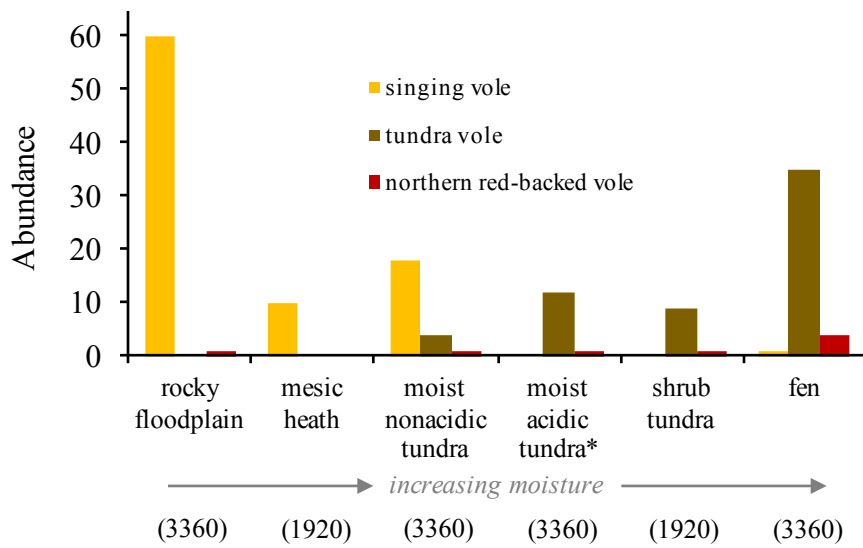
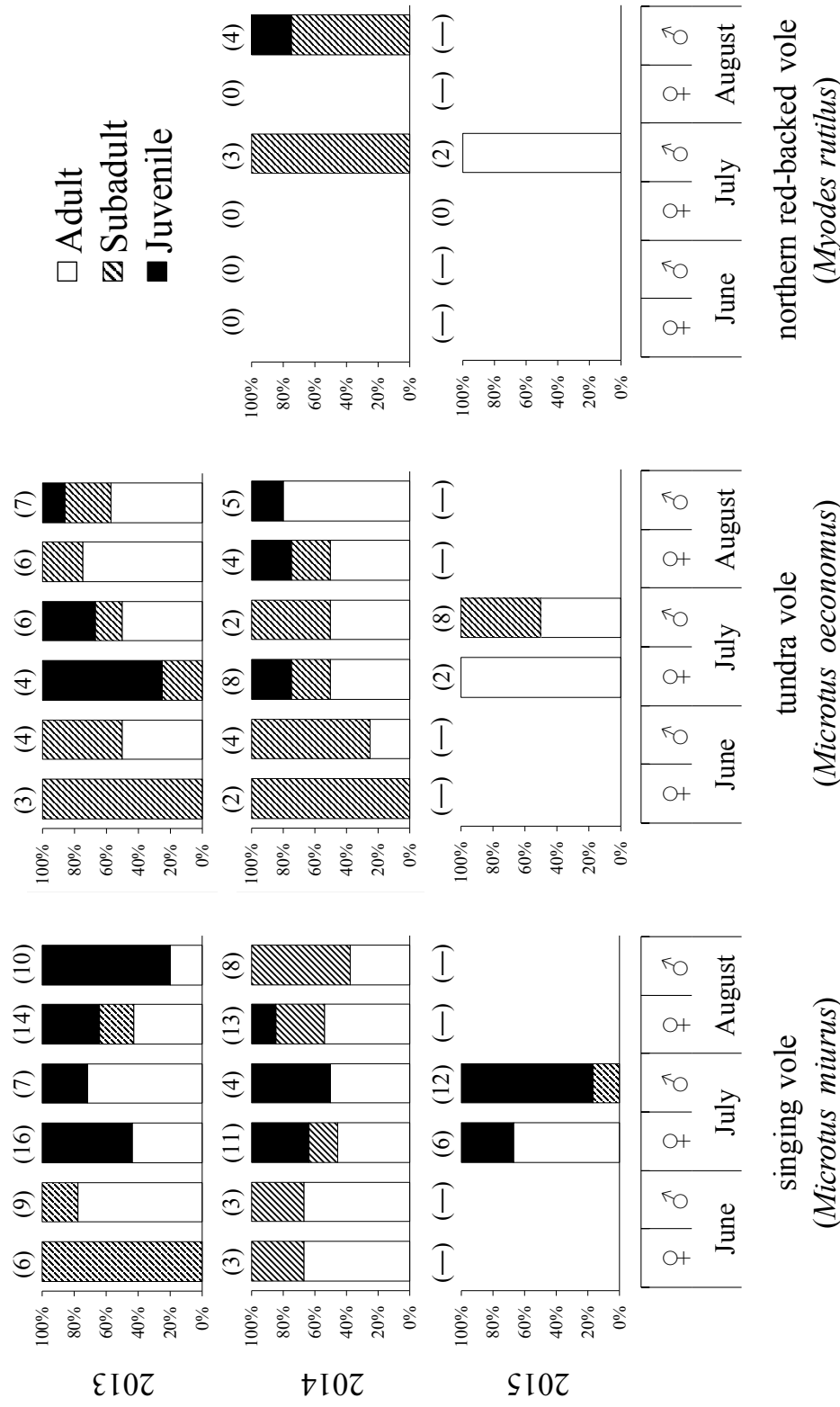


Figure 1.3. Abundance of vole species, aggregated across all sampling sessions (2013 – 2015), by habitat type. Count of trap-nights is displayed below each habitat in parentheses.  
 \*Abundances on moist acidic tundra are aggregated from grids MAT13 and MAT14.

Figure 1.4. Population structure by age and sex for each sampling session (2013 – 2015). In 2015, sampling was conducted in July only (months not surveyed are displayed as “—”). Number captured are shown in parentheses above bars. Age classification is a size-based category following Myllymäki (1977) and Batzli and Henttonen (1990, 1993). For the singing vole and the northern red-backed vole, juveniles were categorized as  $<18g$  and  $\leq 28g$  for females and  $\geq 18g$  and  $\leq 30g$  for males; all larger voles were considered adults. For the tundra vole the same age categories were used except subadults were categorized as  $\geq 19g$  and  $<37g$  for females and  $>10g$  and  $<35g$  for males



singing vole  
(*Microtus miurus*)

tundra vole  
(*Microtus oeconomus*)

northern red-backed vole  
(*Myodes rutilus*)

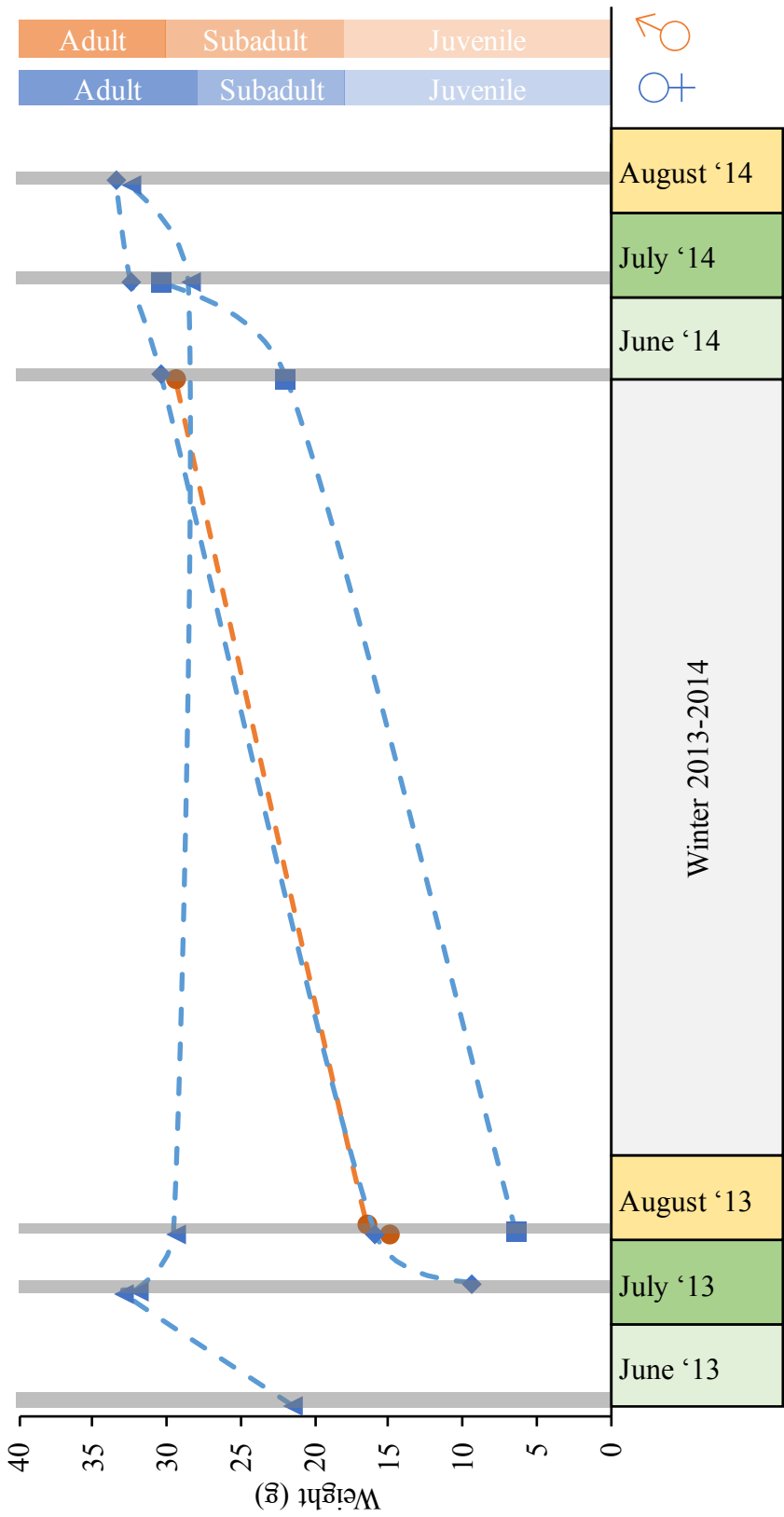


Figure 1.5. Weight progression of four singing voles on the rocky floodplain grid over the course of two consecutive summers. Vertical grey bars in the plot area indicate individual sampling sessions; months are denoted below the horizontal axis. Blue lines and markers indicate female, orange line and markers indicates male.

## **Discussion**

### *Habitat preferences*

Findings from this study (Figure 1.3) reaffirm documented segregation of the singing vole and the tundra vole across habitat types along a moisture gradient in this region (Batzli and Henttonen 1990). The singing vole was most abundant on the most mesic of the surveyed habitats (rocky floodplain), while the tundra vole was most abundant on the wettest of the surveyed habitats (fen). This aligns with habitat preferences documented by Batzli and Henttonen (1990). Moist nonacidic tundra may be considered a transitional habitat based on shifting vole species composition across years. In 2013 this habitat was exclusively occupied by the singing vole, in 2014 both the singing vole and the tundra vole were present at similarly low abundances, and in 2015 the singing vole was dominant to the tundra vole and northern red-backed vole (Table 1.1). There was only one instance of singing vole and tundra vole co-occurrence at a trap-station, in 2015. While a singing vole did occur on the fen (in 2014), it was a subadult male and is considered transient, rather than exhibiting affinity for that habitat type. Northern red-backed voles were found on all habitats except mesic heath, however only the fen was occupied by multiple individuals. This does not support the suggestion by Batzli and Henttonen (1990) that northern red-backed voles prefer rocky or gravelly habitats.

### *Abundance and distribution*

Observed abundances of each microtine species were low across the three years of sampling. For each species, abundance aggregated across all summer sampling periods declined from 2013 to 2014, and comparison between abundances in July 2015 and those in the previous two July sampling sessions indicated population levels were not increasing. Relative abundances

documented here were on the lower end of the range of those documented by Batzli and Henttonen (1990) for the same region. These prior surveys reported relative abundances of tundra voles on wet habitats at >15 per 100 trap-nights (Batzli and Henttonen 1990), whereas this study recorded relative abundances on a similar habitat (fen) at approximately 1 per 100 trap-nights. Similarly, in prior surveys singing voles were recorded at relative abundances of 8, 11, and 10 per 100 trap-nights, respectively on rocky flats, steep slopes, and low slopes, respectively (Batzli and Henttonen 1990), whereas in this study singing voles were recorded at relative abundances at 1.8, 0.5, and 0.5 per 100 trap-nights, respectively, on comparable habitats (RF, MH, MNT).

The northern red-backed vole was rare relative to the singing vole and the tundra vole. The sample population of northern red-backed voles across all sampling sessions was exclusively male. Interestingly, a single subadult northern red-backed vole occupied both the moist acidic tundra grid and the shrub tundra grid near Imnavait creek (documented distance moved was nearly 400 m). Large, overlapping home ranges are common for male red-backed voles (*Myodes* spp.) at low densities (Boonstra and Krebs 2012).

Batzli and Henttonen (1990) provided evidence of restricted habitat use in winters and sub-optimal quality of available winter habitat near Toolik Lake, which they contended may severely reduce survival over the winter and limit substantial population growth in summer. Our documented decline in singing vole abundance from August 2013 to June 2014 indicates low winter survivorship (Figure 1.4). Only three of the 13 singing voles captured as juveniles in August 2013 were recaptured in June 2014, each of these having grown over the winter to reach adult or subadult age class. Only one of the eight adult singing voles captured in August 2013 was recaptured in July and August 2014; as this individual was initially captured as a subadult in



June 2013 it likely had survived the winter preceding 2013 sampling along with winter 2013—2014 (Figure 1.5).

Sign surveys of winter activity conducted in June 2014 while establishing live-trapping survey grids noted evidence of grazed tussocks, winter nests, runways, and latrines from vole activity, particularly at the two Imnavait grids (MAT14, SHRUB). While the age of this sign was not determined, it was judged to be recent, likely from the prior winter. Similarly, the mesic heath site was noted to have abundant sign of vole activity, particularly holes and runways in moss cover and latrines, prior to surveys in June 2014. Subsequent live-trapping at these sites in 2014 yielded surprisingly low captures based on the amount of vole sign observed. Both Krebs et al. (2012) and Pitelka and Batzli (2007) documented instances of high densities of lemming nests followed by very low summer lemming densities, which they hypothesized may indicate variation in winter and spring habitat affinities or concentrated predation in the winter.

### *Demographic trends*

Low sample sizes restricted the ability to statistically interpret trends in age, weight, or reproductive condition of microtine populations across the study, but qualitative summaries are provided (Figure 1.4). In both 2013 and 2014, the sample populations were well balanced by sex for both the signing vole (2013: 22 females, 25 males; 2014: 16 females, 12 males) and the tundra vole (2013: 11 females, 15 males; 2014: 13 females, 11 males). In July 2015, counts were imbalanced by sex for both the signing vole (6 females, 12 males) and the tundra vole (2 females, 8 males). However, sex ratios from counts were often imbalanced within a single sampling session, so these data should be considered in context (Figure 1.4).

### *Impact of extrinsic conditions*

Extrinsic factors likely influenced the low abundances observed throughout this study. Population dynamics of arctic microtine rodents in winters may be dominated by the effects of stochastic climatic events on snow conditions (Ims et al. 2008, Kausrud et al. 2008, Duchesne et al. 2011), in particular snow-pack depth and density (Duchesne et al. 2011, Bilodeau et al. 2013). Arctic microtine population abundance, survivorship, space use, habitat selection, and foraging have been strongly associated with snow conditions (Korslund and Steen 2006, Duchesne et al. 2011, Bilodeau et al. 2013). Mild winters reduce the availability of critical resources by diminishing thermal protection provided by the snowpack and by limiting access to quality food within a subnivean layer fragmented by freezing rain. Similarly, mild winters may increase both microtine drowning from flooding and exposure to predators, increasing stress on voles in winter and consequently limiting reproductive potential in the subsequent breeding season (Korslund and Steen 2006, Hoset et al. 2009, Duchesne et al. 2011).

Krebs et al. (2002) speculated that the interaction of winter weather and vegetation structure has substantial impacts on the quality of the subnivean layer, and that lemmings in northern Canada select wintering sites based on structural features more than on food availability. Moreover, heterogeneous microtopography, increased slope, and greater snow depth at the landscape level provide a more favorable microclimate (Duchesne et al. 2011) to lemmings in northern Canada. Near Toolik Lake, Batzli and Henttonen (1990) noted that singing voles placed haypiles at rocky sites and at the base of shrubs, while tundra voles nested most frequently at the wettest habitat types (wet swales and watercourses). However, a study in Nunavut, Canada showed that wet, low habitats (analogous to the tundra vole-dominated fen habitat near Toolik Lake) had a negative relationship with snowpack depth and a lower

proportion of lemming nesting sites compared to mesic habitats with heterogeneous microtopography (Duchesne et al. 2011).

This suggests that the combination of vole winter habitat selection and variance in snowpack quality related to habitat structure may have contributed to differences in abundance between the singing vole and the tundra vole near Toolik Lake. Specifically, heterogeneous microtopography at the rocky floodplain grid may have facilitated superior snowpack conditions for the singing vole population whereas the lack of heterogeneous microtopography at the fen grid may have diminished snowpack quality for the tundra vole population. 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 climatic events have on microtine population dynamics in the northern foothills of the Brooks Range.

#### *Cyclicality of microtine populations*

The duration of this study was insufficient to comment on cyclicality in microtine populations and whether populations cycles are dampening in the northern foothills of the Brooks Range, as suggested by studies on microtine population dynamics in Scandinavia (Ims et al. 2008, Kausrud et al. 2008). However, considering the three consecutive low-population years across the study sites, and the precedent of 3-5 year regular population cycles documented in many arctic microtine rodents (reviewed in Korpimäki et al. 2004), continued research on population dynamics would provide an opportunity to address that issue in this region. Studies indicate that the legacy of high population densities in the summer may facilitate winter survival, as higher densities may keep more runways free of ice in the winter, improving access to food

(Korslund and Steen 2006, Hoset et al. 2009). Considering this point, vole densities may have remained low throughout this study because the surviving individuals were less effective at runway maintenance during winters, restricting space use.

Optimal winter conditions and absolute reproductive capacity allow for extreme peaks in population abundance, which Kausrud et al. (2008) cite as the reason for lemming (as opposed to other microtine taxa) dominance in a Norwegian alpine habitat. However, Korpela et al. (2013) argue that mild winters are not uniformly dampening cyclicality across arctic regions, rather, microtine populations dynamics were more correlated with growing season than with winter conditions. While such studies on the correlation of population dynamics with mild winter conditions and growing season were conducted in Scandinavia, little research has been conducted recently on the North Slope of Alaska. Continued monitoring of demographic trends may offer critical insight into the cyclicality of microtine populations across this landscape. The consequence of absent periodic or even occasional dramatic spikes in microtine population levels and the co-occurring intensity of grazing will alter the disturbance regime on plant communities across the tundra (Kausrud et al. 2008).

## CHAPTER II

### SPACE USE AND HABITAT AFFINITIES OF A SINGING VOLE POPULATION

#### **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. On the northern foothills of the Brooks Range, Alaska, a treeless region underlain by continuous permafrost with a mosaic of tundra plant communities, five species of microtine rodents (subfamily Arvicolinae, e.g., voles and lemmings), occur. The tundra (or root) vole (*M. oeconomus*) and the singing vole (*Microtus miurus*) are co-dominant species, while a third vole species, the northern red-backed vole (*Myodes rutilus*) and two lemming species, the collared lemming (*Dicrostonyx groenlandicus*) and the brown lemming (*Lemmus trimucronatus*), are present but rare (Bee and Hall 1956, Batzli and Henttonen 1990). Whereas the tundra vole has been extensively studied across its Holarctic range, the singing vole is a Nearctic species that has been less extensively studied. These species 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 tundra vole prefers wet-moist (i.e., poorly-drained) habitats (Galindo and Krebs 1985, Batzli and Henttonen 1990, 1993, Batzli and Lesieutre 1991, 1995, and see this thesis, Chapter 1). Because of this spatial segregation, population dynamics can be examined as a single species system without the confounding factors of interspecific interactions. Here, I focus

on characterizing space use by the singing vole, the lesser studied co-dominant vertebrate herbivore on the northern foothills of the Brooks Range, in the context of changing climatic conditions and subsequent shifts in habitat.

Whereas a prior study conducted at this site addressed singing vole home range and social organization (Batzli and Henttonen 1993), questions on the impacts of intraspecific interactions, microhabitat affinities, and stochastic winter climate events related to space use remain. Notably, the singing vole is unique among microtine rodents in its tendency to both cooperatively build haypiles above ground (Batzli and Henttonen 1993) as well as cache food underground (Cole and Wilson 2010), highlighting the importance of habitat affinities that facilitate such food provisioning along with intraspecific interactions in the dynamics of its space use. While the singing vole occurred on two other mesic habitats contemporaneously surveyed, relative abundance of this population was substantially greater than others (Batzli and Henttonen 1990, this thesis, Chapter 1), suggesting local-scale habitat heterogeneity and microhabitat affinities may promote comparative resilience to extrinsic pressures. Furthermore, extensive home range overlap was previously documented for this population of singing voles (Batzli and Henttonen 1993). In order to thoroughly assess patterns of space use by the singing vole, the roles of intraspecific interactions and microhabitat affinities must be considered.

I report the findings of an intensive mark-recapture survey of a singing vole population on rocky floodplain tundra habitat near Toolik Field Station, conducted over two consecutive summers. My objectives were: 1) document annual variation in singing vole population density; 2) assess size, overlap and intensity of use within core areas of singing vole home ranges; 3) and assess microhabitat affinities 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 singing vole space use and interactions with plant communities.

## **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 above sea level) in 2013 and 2014. In June 2013 a mark-recapture grid was established on a rocky floodplain (RF) near the outlet stream of Toolik Lake (Figure 2.1). 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 4 parallel trap-lines with a trap station set every 10 m for a total of 60 stations across the 30m x 140m array. Two Sherman live traps (H. B. Sherman, Tallahassee, Florida, USA) 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 senescence. In each session, sampling was conducted for four consecutive nights. Traps were checked approximately every six hours (midnight, morning, midday, evening), which reduced incidental mortality from trap-stress or exposure. Across each summer season the grid was surveyed for 1,440 trap-nights, with a total of 5,040 trap-checks.

Upon capture each individual was identified to species, sexed, aged (juvenile, sub-adult, adult), examined for reproductive condition, weighed (using a Pesola® scale), and marked with a Passively Integrated Transponder (PIT) tag. Singing voles  $\leq 18$  g were classified as juveniles,

females 18 g – 28 g and males 18 g – 30 g as subadults, and females > 28 g and males > 30 g as adults (Batzli and Henttonen 1990, 1993). Age was categorized based on weight, such that subadult did not refer to reproductive status (*sensu* Myllymäki 1977). Field procedures follow guidelines of the American Society of Mammalogists (Sikes and Gannon 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 x 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, deciduous shrub). Vegetation cover data were assumed to be representative of the area surrounding each trap station.

#### *Population density estimation*

Population abundance of singing voles was estimated using a robust design Huggins closed-captures model 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 assumes that the sample population was closed (i.e., no temporary immigration, emigration, births, or deaths) during each sampling session (i.e., over the four consecutive nights). Encounters 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. The effective area sampled, accounting for area sampled beyond the extent of the grid, was calculated for each year by using



half the mean maximum distance moved by the sample population to add a boundary strip to the grid (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 within a year were aggregated for each individual and home range analysis was conducted for each vole encountered  $\geq 5$  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. Following common practice, only female singing voles were modeled due to the documented large home range size and tendency of male singing voles to shift home ranges during the summer (Batzli and Henttonen 1993). Additionally, only those 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.

Home range models were constructed using the ‘adehabitatHR’ package (Calenge 2006) in R (R Core Team 2015). Minimum convex polygons (MCPs) were initially constructed to facilitate comparison with singing vole home range estimates calculated by Batzli and Henttonen (1993) from this site using data from the 1980s, and to compare with kernel density approaches. A kernel density estimator was used to model utilization distributions (UDs) for each vole. The UD displays the probability density of relocating a vole given coordinates (Va Winkle 1975, Silverman 1986, Seaman and Powell 1996, Calenge 2011). Unlike MCPs, UDs are 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<sub>s</sub> (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 utilization distribution 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), distinguishing it from the periphery of the home range. 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 ( $0 \leq \text{UD volume} \leq 1$ ). 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 (Figure 2.2). 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, 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 B).

Core areas and 95% UDs (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 within cores were classified as either “shared” or “exclusive” based on whether they were included in the core areas of multiple singing voles within a given year (“shared”) or in the core area of only the focal singing vole within a given year (“exclusive”). Total encounters at “shared” trap stations and at “exclusive” trap stations within cores were divided by the total available trap stations within each category, 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 relative to habitat type and availability.

### *Habitat affinity*

The distribution of vole encounters across the 60 trap stations were compared 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 habitat affinity on space use, use of trap stations was analyzed in correspondence with vegetation cover data. Habitat affinities were characterized by considering the relationship between cover composition and encounters at each trap station.

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 ( $\beta = -0.25$ ) 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).

Observed use (aggregate encounters) of each microhabitat was compared relative to its availability (number of trap stations characterized as 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-square tests were run to compare the observed use of microhabitats by the sample population to the expected use (proportional to availability) 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).

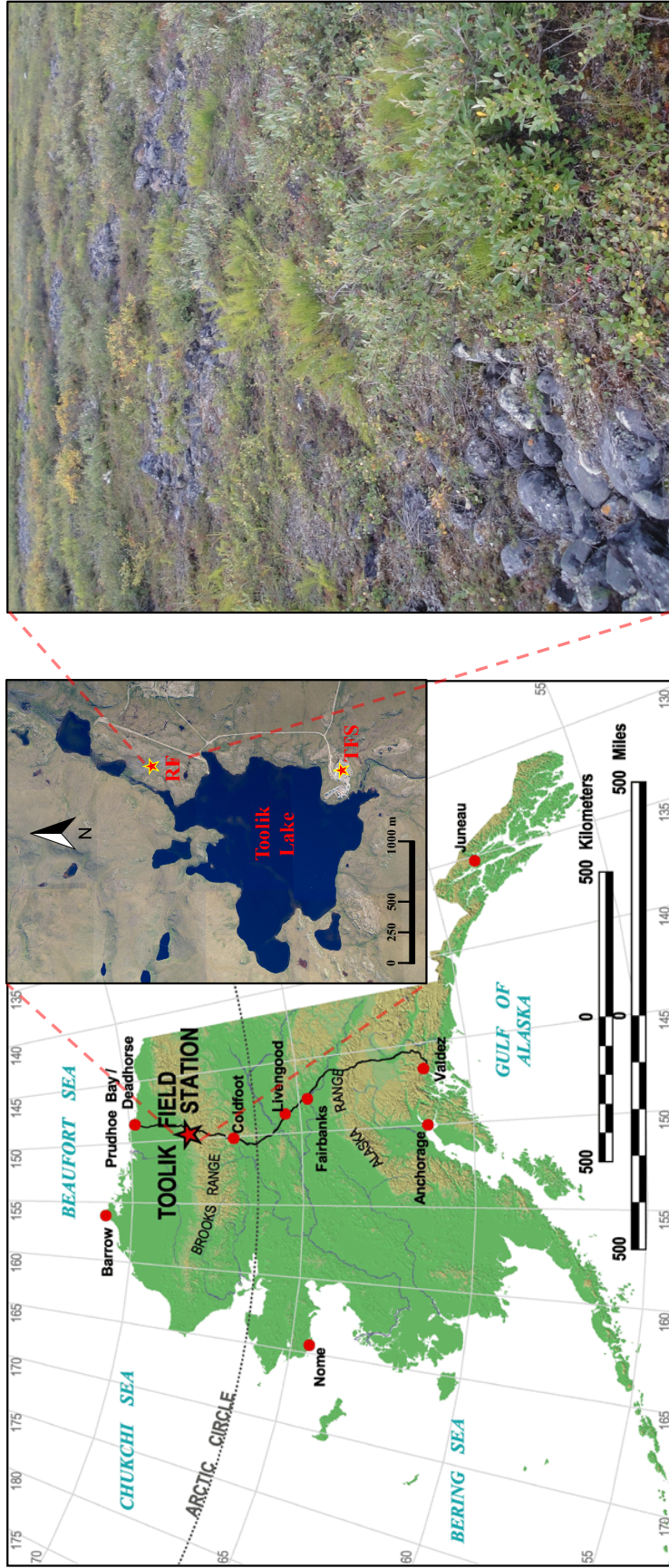


Figure 2.1. Locations of 0.42 ha rocky floodplain grid (RF), Toolik Lake, and Toolik Field Station (TFS) (inset) in Alaska (left panel). Base map provided by Toolik Field Station GIS Department. The photograph (right panel) provides an example of mosaic microhabitats on the rocky floodplain.

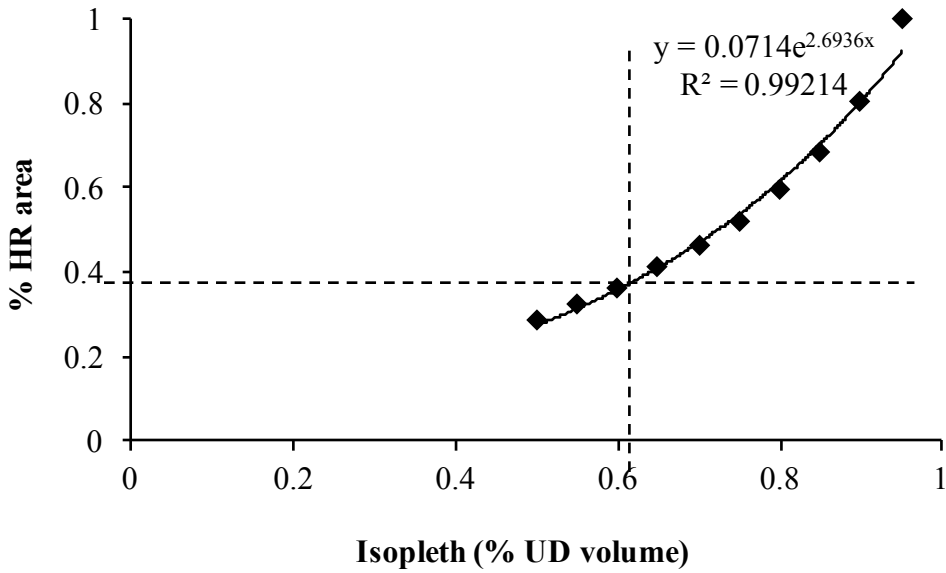


Figure 2.2. The utilization distribution (UD) isopleth delineating core area was calculated by determining where the first derivative of the curve equals 1. For this individual, the UD isopleth delineating core area was 61.2%, which represented 37.2% of the total home range area.

## Results

### *Activity patterns and population density estimates*

Singing voles were active throughout the day, though singing voles 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). Tripped traps were common throughout sampling (11% and 24% of trap-checks in 2013 and 2014, respectively), particularly at the midday and evening checks.

Abundance estimates of singing voles on the rocky floodplain from the Huggins closed-captures model ranged from 10.45 to 25.09 ( $\pm 0.71 - 2.07$  SE) across Summer 2013 and from 5.13 – 14.35 ( $\pm 0.36 - 0.62$  SE) across Summer 2014. All count and abundance estimates data are reported in Appendix A. The effective sampling area was estimated as 0.5602 ha and 0.5720 ha in 2013 and 2014, respectively; these areas were used to calculate densities from the abundance estimates. While population density within a sampling session was on average  $45 \pm 4\%$  SE lower in 2014 than in 2013, the general trend of population density increasing from June to August was consistent between years (Figure 2.3).

### *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 Appendix B. A linear regression of the 17 individuals for which home ranges were modeled showed that 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 were not significantly different

between 2013 and 2014 (two-sample  $t(df = 9) = 1.11, p = 0.30$ ). Average minimum convex polygon (MCP) area was not significantly different between 2013 and 2014 (two-sample  $t(df = 7) = 0.81, p = 0.44$ ). Using kernel density estimators, home range size (95% isopleth) and core area (61% isopleth) were estimated from the utilization distribution (UD) for each vole (Figure 2.4). Average core area was not significantly different between 2013 and 2014 (two-sample  $t(df = 8) = 0.26, p = 0.80$ ). Average proportion of home range as core was not significantly different between 2013 and 2014 (two-sample  $t(df = 15) = -0.48, p = 0.64$ ). Average relative intensity of use within core areas (61% isopleth divided into proportion of home range delineated as core) was not significantly different between 2013 and 2014 (two-sample  $t(df = 14) = 0.02, p = 0.98$ ). Average area of core shared with other modeled core areas was  $394 \pm 111 \text{ m}^2 \text{ SE}$  in 2013 and  $467 \pm 87 \text{ m}^2 \text{ SE}$  in 2014 (example shown in Figure 2.5).

One individual was relocated in both 2013 ( $n = 16$ ) and 2014 ( $n = 10$ ) and its core areas from 2013 ( $406 \text{ m}^2$ ) and 2014 ( $658 \text{ m}^2$ ) overlapped by  $139 \text{ m}^2$ . 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 aggregate encounters across trapping stations was not significantly correlated between years ( $r^2 = 0.04, F = 2.54, p = 0.12$ ) (Figure 2.6). Within the sub-population 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 stations within core areas was assessed for both 2013 and 2014 (Table 2.1). Chi-square 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 ( $\chi^2 = 0.84$ ,  $df = 1$ ,  $n = 82$ ,  $p = 0.36$ ).

### *Habitat Classification*

Hierarchical cluster analysis of vegetation cover data produced a dendrogram (Appendix C, S2.1) which 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 – 21 trap stations. Dominant or co-dominant cover types were used as labels for microhabitats (Figure 2.7), based on average vegetation cover composition of all trap stations in that microhabitat (Appendix C, S2.2). Microhabitats on this grid were distinct, as exhibited by the long stems separating most groups on the dendrogram.

### *Microhabitat affinity*

Use of microhabitats at the population level was assessed for both years (Table 2.2). In 2013 the overall use of microhabitats by the population was disproportionate to their availability ( $\chi^2 = 55.50$ ,  $df = 4$ ,  $n = 132$  encounters,  $p < 0.001$ ), while in 2014 the overall use of microhabitats by the population was marginally disproportionate to availability ( $\chi^2 = 31.99$ ,  $df = 4$ ,  $n = 120$ ,  $p = 0.052$ ). Across 2013 and 2014, microhabitat categories SHRUB ( $\chi^2 = 6.72$ ,  $df = 1$ ,  $n = 70$ ,  $p < 0.01$ ), BARE ( $\chi^2 = 4.47$ ,  $df = 1$ ,  $n = 39$ ,  $p = 0.035$ ), and BARE + OTHER ( $\chi^2 = 14.76$ ,  $df = 1$ ,  $n = 41$ ,  $p < 0.001$ ) were each used differently than expected based on availability.

Use of microhabitats within core areas was assessed for both 2013 and 2014 (Table 2.3). Chi-square 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,  $p = 0.02$ ), while in 2014 the overall use of trap stations by microhabitat category within combined core areas ( $n = 10$ ) was not disproportionate to their availability ( $\chi^2 = 2.50$ ,  $df = 4$ ,  $n = 82$ ,  $p = 0.64$ ).

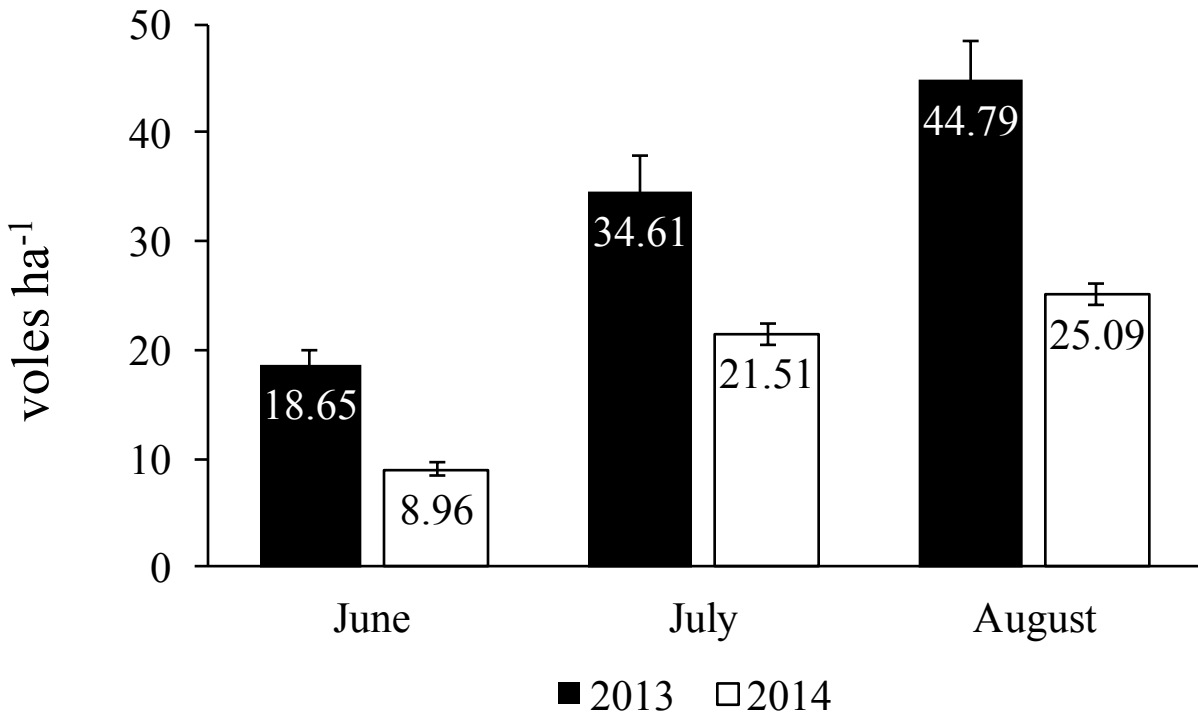
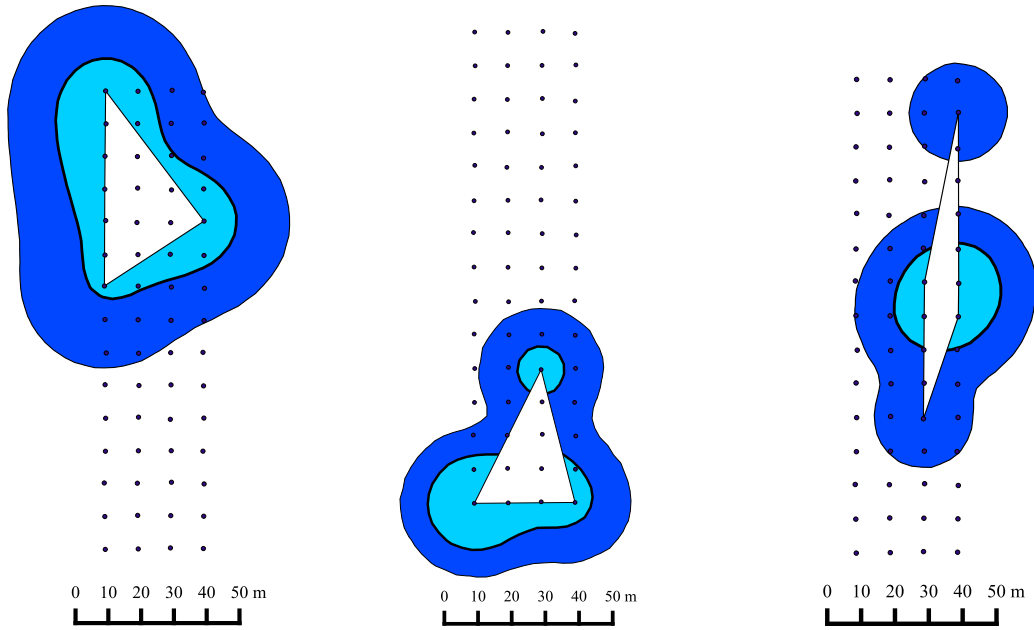
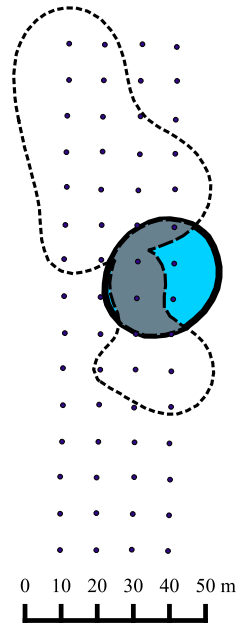


Figure 2.3. Mean density estimates ( $\pm$  SE) of singing voles (no. ha<sup>-1</sup>) on the rocky floodplain by sampling session in 2013 (black) and 2014 (white).



*Figure 2.4. Models of home range (95% isopleth of the utilization distribution, dark blue), core area (61% isopleth of the utilization distribution, light blue), and minimum convex polygon (MCP, white) of 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.*



*Figure 2.5. Model of exclusive and shared space of one adult female singing vole (solid thick border) (core area: 786 m<sup>2</sup>). Exclusive core space of this individual is shown in blue (351 m<sup>2</sup>, 45% of core area); space it shares with the core areas of two other female singing voles is shown in grey (435 m<sup>2</sup>, 55% of core area). The remainders of the core areas of those two individuals (one above, one below) are outlined with dashed borders. Trap stations are overlaid for reference.*

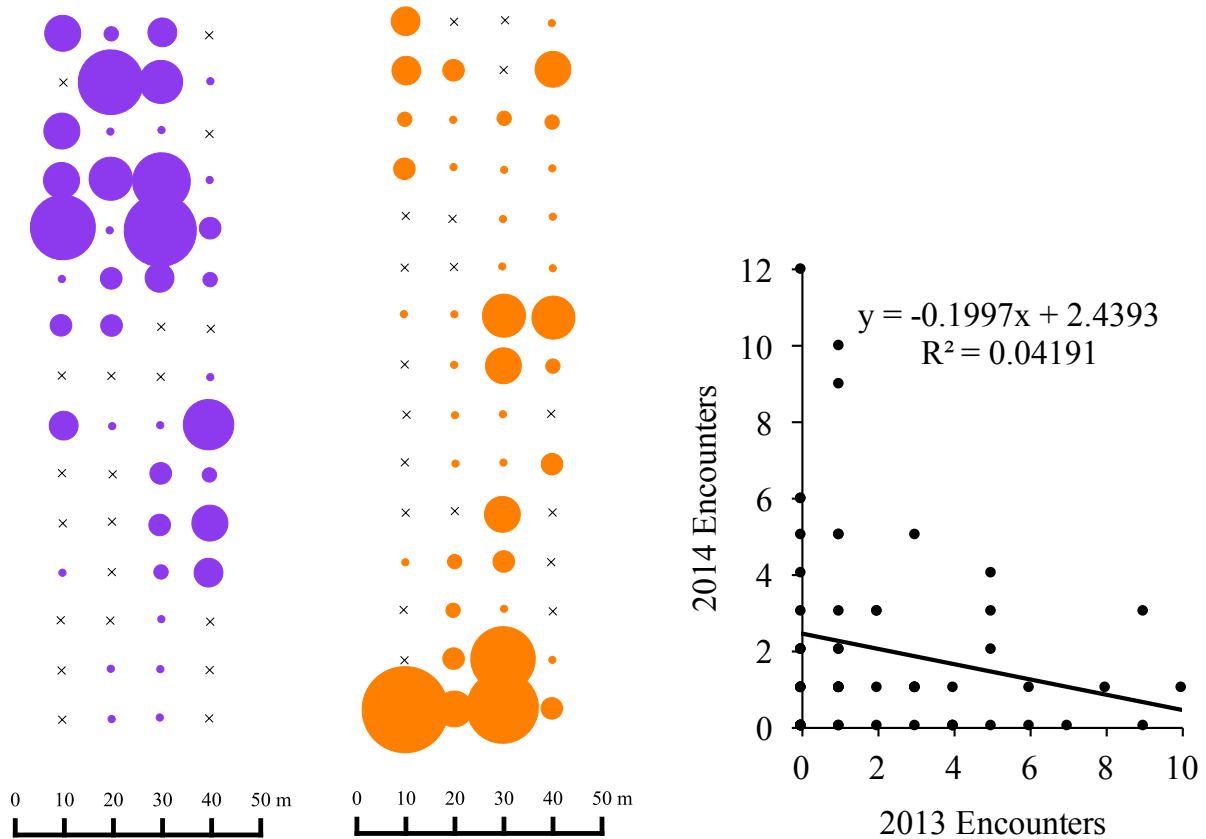


Figure 2.6. Distribution of singing vole encounters by trap station on the rocky floodplain grid in 2013 (left panel, purple circles, 132 aggregate encounters) and in 2014 (middle panel, orange circles, 120 aggregate encounters). Size of each circle corresponds to number of encounters at a trap station, ranging from 1 – 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 2.1. Available trap stations, observed encounters, and expected encounters of singing voles by exclusive and shared classification within core areas on the rocky floodplain grid in 2013 and in 2014. \* Indicates significant difference from expected values (at  $p < 0.05$ ).*

	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

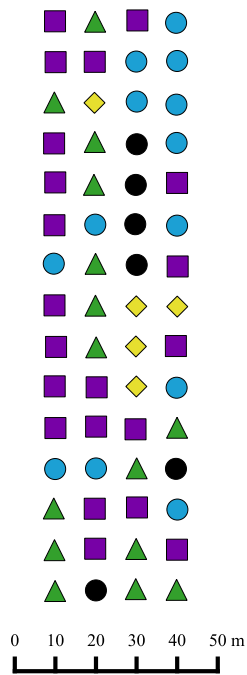


Figure 2.7. Trap stations on the rocky floodplain grid coded by microhabitat: EVEN (purple squares, n = 21), SHRUB (green triangles, n = 15), BARE (blue circles, n = 13), BARE + OTHER (black circles, n = 6), and EQUISETUM (yellow diamonds, n = 5).



Table 2.2. Available trap stations, observed encounters, and expected encounters of singing voles by microhabitat category on the rocky floodplain grid in 2013 and in 2014. \* Indicates significant difference from expected values (at  $p < 0.05$ ).

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

Table 2.3. Available trap stations, observed encounters, and expected encounters of singing voles by microhabitat category within combined core areas on the rocky floodplain grid in 2013 and in 2014. \* Indicates significant difference from expected values (at  $p < 0.05$ ).

	EVEN	SHRUB	BARE	BARE + OTHER	EQUISETUM
2013 ( $n = 7$ 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 ( $n = 10$ 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

## Discussion

### *Activity patterns and population density*

While microtines are generally nocturnal or crepuscular (active at dusk and dawn), sampling occurred during the arctic summer (daylight is continuous from late May through mid July), and data on timing of captures suggested singing voles were generally active throughout the day. Tripped traps, most frequently occurring at midday and evening checks were noted as a factor possibly reducing captures rate on the rocky floodplain grid by limiting the number of traps accessible to voles. Arctic ground squirrels (*Urocitellus parryii*) were the main cause of tripped traps, and they were frequently observed removing bait from traps while juvenile squirrels were incidentally captured in traps on occasion.

Population density estimates of singing voles were within the range reported by Batzli and Henttonen (1993) on the same rocky floodplain. June density from 2013 ( $18.65 \text{ ha}^{-1}$ ) aligned with June densities from 1985 ( $16.7 \text{ ha}^{-1}$ ) and 1986 ( $18.6 \text{ ha}^{-1}$ ) and August density from 2013 ( $44.79 \text{ ha}^{-1}$ ) aligned with August densities from 1984 ( $44.9 \text{ ha}^{-1}$ ) and 1985 ( $47.1 \text{ ha}^{-1}$ ). However, population density estimates from June and August 2014 ( $8.96 \text{ ha}^{-1}$  and  $25.09 \text{ ha}^{-1}$ , respectively) were higher than the corresponding August 1986 and June 1987 densities ( $3.9 \text{ ha}^{-1}$  in both months), which documented a collapse. Moreover, the population density decline observed in the 1980s occurred over the course of a summer (1986), whereas the decline observed in this study occurred over the winter (2013-2014). Population densities observed during this study were within the range of densities ( $0\text{-}50 \text{ ha}^{-1}$ ) reported by all studies on the singing vole (Cole and Wilson 2010).

### *Stability in home range dynamics*

Mean minimum convex polygon (MCP) size of female adult and subadult singing voles ( $n = 28$ ) reported by Batzli and Henttonen (1993) ranged from 366 – 775 m<sup>2</sup> in 1984 – 1987. In comparison, mean MCP area of female adult and subadult singing voles ( $n = 17$ ) reported here ranged from 345 m<sup>2</sup> – 595 m<sup>2</sup> in 2013 - 2014.

Minimum convex polygons (MCP) underestimated home range areas compared to kernel density estimators (KDE). Additionally, variance in MCP area between years was substantially greater than KDE area. MCP size decreased by 42% from 2013 to 2014, whereas mean home range size from kernel density estimation (KDE) at 95% isopleth of the utilization distribution (UD) and mean core area size from KDE at 61% UD decreased by only 15% and 14% from 2013 to 2014, respectively. Moreover, KDE core area at 61% UD contained on average 74% and 85% of known relocations in 2013 and 2014, respectively (Appendix B). Comparison 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 kernel density estimation 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.

Consistency in core area size, proportion of home range area as core area, and intensity of use in core area between 2013 and 2014, despite the decline in population density, suggests that singing vole core area dynamics were not impacted by population density, supporting the contention by Batzli and Henttonen (1993) that home range size of the singing vole was not related to density.

## *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. For singing voles, my findings indicate that not all core areas were continuous. This suggests that those individuals exhibited patchy, concentrated activity within their home ranges (Figure 2.4). The high concentration of activity within shared portions of individual core areas (Table 2.1) suggests that interactions between singing voles within shared core areas were important in structuring space use. However, microhabitats were distinct and sharply defined (Appendix C, Figure S2.1), albeit patchily distributed (Figure 2.7), on the rocky floodplain, which suggests that both habitat preference and social interactions may have a balanced influence on space use by the singing vole. Galindo and Krebs (1985) suggest 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 habitat affinities by this population of singing voles did not indicate that habitat suitability was related to density, as assessed by interannual changes, suggesting resources may not be limited on this habitat.

The vegetation sampling indicated that the rocky floodplain was a mosaic of microhabitats for which singing voles exhibited significant affinities; however, the presence of other singing voles also influenced space use, thereby implicating social interactions as a plausible driver of space use. In 2013 space use by individuals was significantly impacted by both social interactions (documented by use of trap stations shared by multiple core areas) and

microhabitat affinities (use of microhabitats within core areas). Concentrated space use by multiple individuals and cooperative resource acquisition (e.g., haypiles built by multiple individuals) exhibited by the singing vole (Batzli and Henttonen 1993) may aid in its persistence under winter conditions through maintenance of subnivean space and access to food caches, as documented for the tundra vole (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 among multiple individuals 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 (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 (Figure 2.6).

### *Habitat affinities*

The microhabitat types of the rocky floodplain were diverse and clustered along a gradient of bare rock cover (Appendix C). This is in contrast to other tundra habitat types of the northern foothills of the Brooks Range which showed higher levels of homogeneity (this thesis, Chapter 1). Composition of both the rocky floodplain overall and the combined core areas in terms of microhabitat types was similar. This suggests that the distribution (i.e., patchiness) of microhabitats across the grid occurs at the scale of core areas, 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 non-dominant 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 and Rowe, *unpublished data*) and in the findings of Batzli and Henttonen (1990) indicated that singing voles likely nest under the rocks and boulders.

It is possible that the characterization of microhabitats using only composition of vegetation cover masks the importance of access to bare rock, even on a broad level. The BARE microhabitat, dominated by bare rock, was under-utilized in both years at both the population level and within core areas. 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 at a local scale over the BARE microhabitat. 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 disproportionately to availability.

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, dominated by *Equisetum* spp., was never over-utilized, neither at the population level nor at the 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, and 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 at a local scale, over higher levels of either highly palatable food (e.g., *Equisetum* spp.) or structural cover (rocks and boulders).

## **Conclusions**

The findings presented here suggest both social interactions and heterogeneous habitat 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 grid is such that it allows singing voles to access a variety of vegetation cover types, both within and among the microhabitat categories, on the scale of an individual's core area. 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. Further research addressing the interactive effects of social behavior, relatedness, specific habitat features, and diet on singing vole populations may clarify the dynamics of space use.



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## APPENDIX A

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.

	Count	Abundance Estimate			
		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	12.30	0.57	12.03 / 15.41	
August	14	14.35	0.62	14.03 / 17.64	

## APPENDIX B

Summary statistics on home range analyses for female subadult and adult singing voles on the rocky floodplain. Only individuals captured  $\geq$  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 (n = 7)				
# Encounters	11.43	2.14	5	18
# Unique relocation points	7	1.4	3	13
MCP area [m <sup>2</sup> ]	595	295	52	2290
Total HR area (95% UD) [m <sup>2</sup> ]	3031	1495	531	11,897
Core area (61% UD) [m <sup>2</sup> ]	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 <sup>2</sup> ]	394	111	0.31	846
2014 (n = 10)				
# Encounters	8.8	1.04	6	15
# Unique relocation points	5	0.26	4	6
MCP area [m <sup>2</sup> ]	346	86	6	905
Total HR area (95% UD) [m <sup>2</sup> ]	2588	575	852	6892
Core area (61% UD) [m <sup>2</sup> ]	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 <sup>2</sup> ]	467	87	95	943

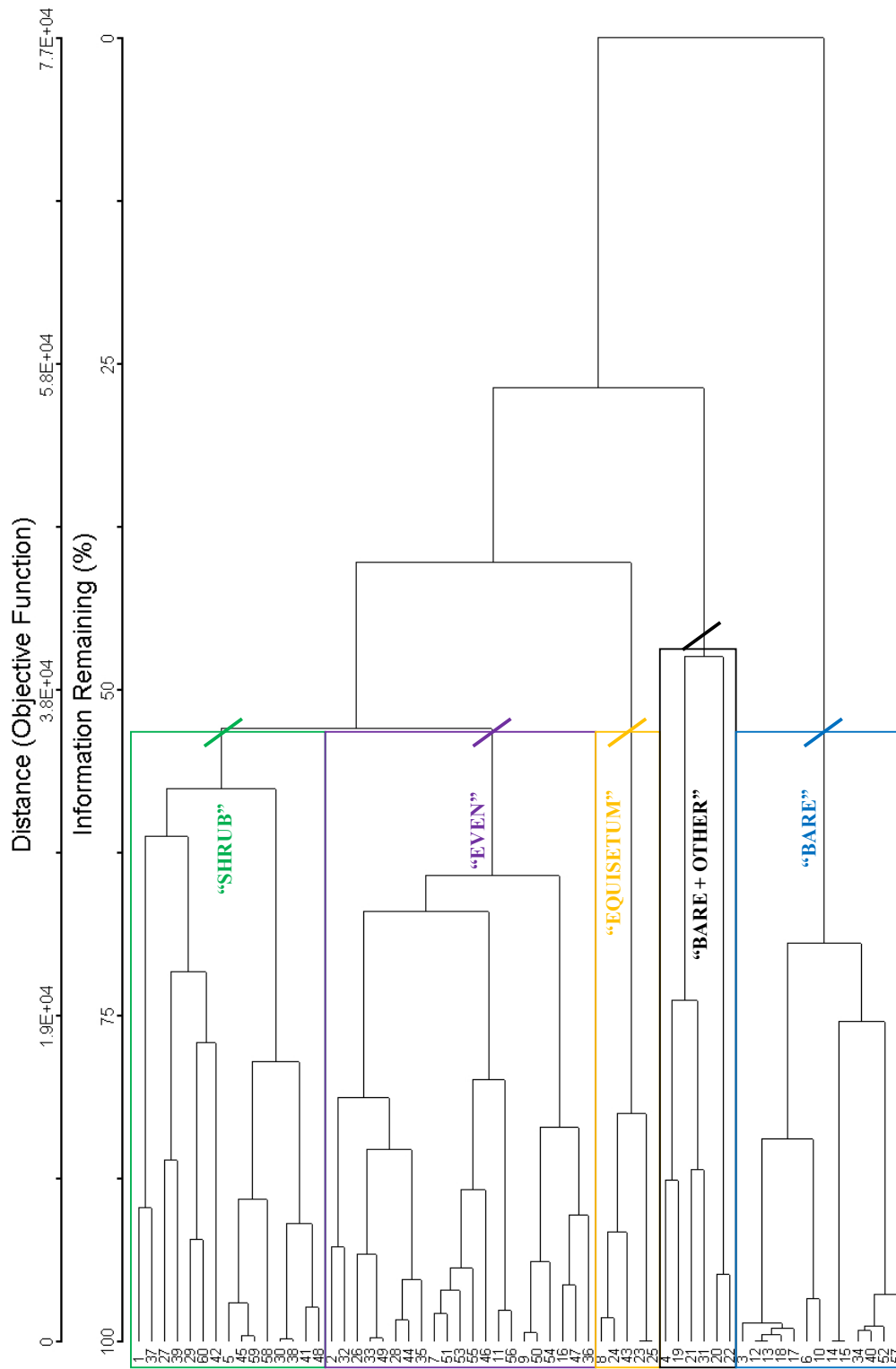


Figure S2.1. Dendrogram from hierarchical cluster analysis of vegetation cover composition of trap stations on the rocky floodplain grid. The dendrogram was initially cut at 53% information remaining. Two groups were then joined at 47% information. Microhabitats are labeled by the average dominant cover type of the average composition of the trap stations (Figure S2.2).



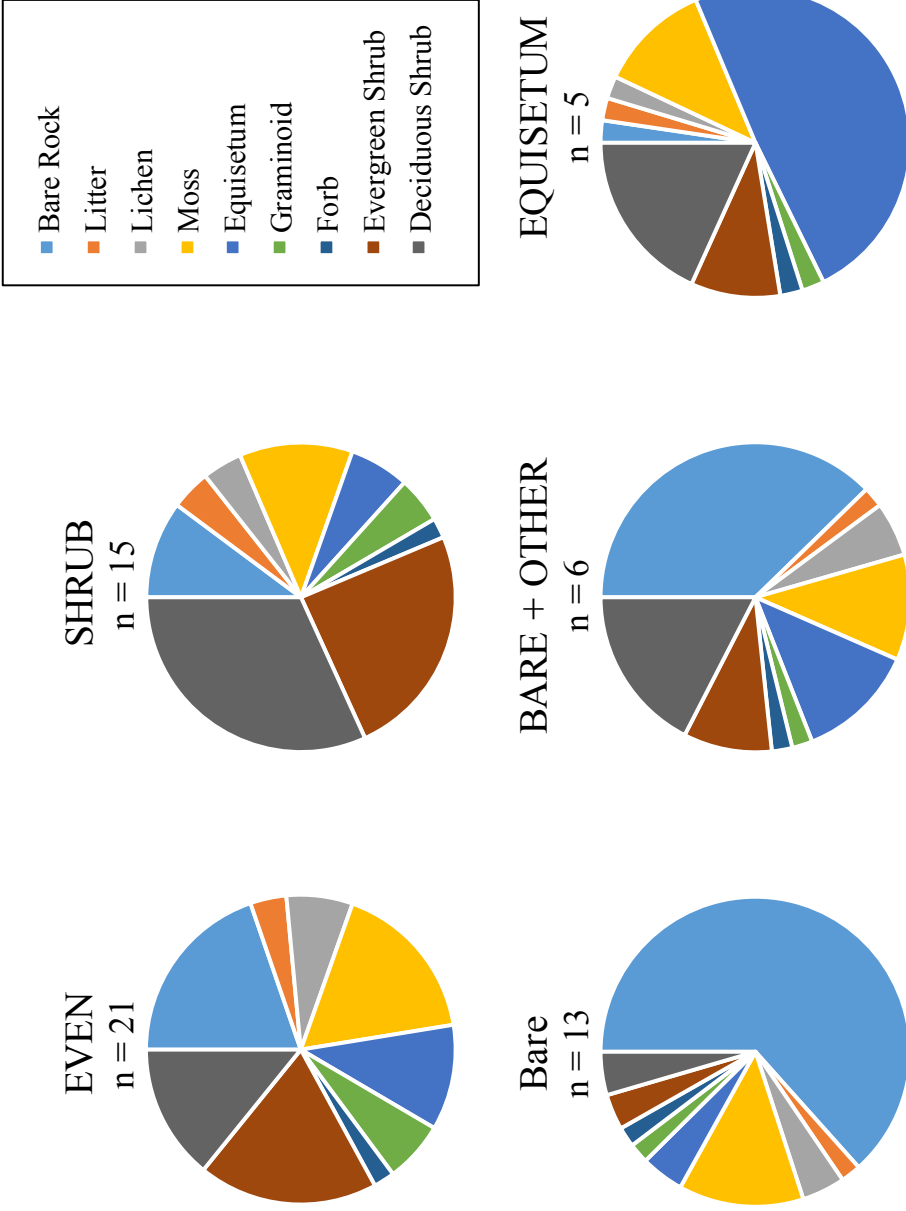


Figure S2.2. Mean vegetation cover composition of trap stations in each microhabitat category from nine cover types.

## APPENDIX D

### University of New Hampshire

Research Integrity Services, Service Building  
51 College Road, Durham, NH 03824-3585  
Fax: 603-862-3564

21-Mar-2013

Rowe, Rebecca J  
Natural Resources & the Environment, James Hall Rm 136  
Durham, NH 03824

**IACUC #:** 130205

**Project:** Small Mammal-Plant Interactions in the Warming Arctic

**Category:** D

**Approval Date:** 21-Mar-2013

The Institutional Animal Care and Use Committee (IACUC) reviewed and approved the protocol submitted for this study under Category D on Page 5 of the Application for Review of Vertebrate Animal Use in Research or Instruction - *Animal use activities that involve accompanying pain or distress to the animals for which appropriate anesthetic, analgesic, tranquilizing drugs or other methods for relieving pain or distress are used.* The IACUC made the following comment(s) on this protocol:

1. In Section II, F of the application, the IACUC checked "Other" and added "Ear punch and hair sample."
2. In Section IV, A, the IACUC added at the end of the sixth sentence of the fourth paragraph, "and a hair sample will be taken."
3. The investigator needs to ensure that all personnel involved in conducting the field study are adequately protected against hazards. UNH IACUC guidance, *Occupational Safety in Field-Based Projects*, is available at [http://unh.edu/research/sites/unh.edu.research/files/docs/RIS/occ\\_safety\\_field\\_based\\_projects.pdf](http://unh.edu/research/sites/unh.edu.research/files/docs/RIS/occ_safety_field_based_projects.pdf)

Approval is granted for a period of three years from the approval date above. Continued approval throughout the three year period is contingent upon completion of annual reports on the use of animals. At the end of the three year approval period you may submit a new application and request for extension to continue this project. Requests for extension must be filed prior to the expiration of the original approval.

**Please Note:**

1. All cage, pen, or other animal identification records must include your IACUC # listed above.
2. Use of animals in research and instruction is approved contingent upon participation in the UNH Occupational Health Program for persons handling animals. Participation is mandatory for all principal investigators and their affiliated personnel, employees of the University and students alike. Information about the program, including forms, is available at <http://unh.edu/research/occupational-health-program-animal-handlers>.

If you have any questions, please contact either Dean Elder at 862-4629 or Julie Simpson at 862-2003.

For the IACUC,



Jill A. McGaughy, Ph.D.  
Chair

cc: File