Canadian Journal of Zoology
Revue canadienne de zoologie

**Quantifying trophic niche spaces of small mammals using
stable isotopes
($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) at two scales across Alaska**

Journal:	<i>Canadian Journal of Zoology</i>
Manuscript ID:	cjz-2015-0025.R1
Manuscript Type:	Article
Date Submitted by the Author:	28-Apr-2015
Complete List of Authors:	Baltensperger, Andrew; University of Alaska Fairbanks, Biology and Wildlife Huettmann, Falk; Institute of Arctic Biology, Biology and Wildlife Department Hagelin, Julie; Alaska Department of Fish and Game, Wildlife Diversity Program Welker, Jeffrey; University of Alaska Anchorage, Biological Sciences
Keyword:	COMMUNITIES/DEMOGRAPHICS < Discipline, ISOTOPES < Discipline, PREY SIZE/DIET COMP. < Discipline, ARCTIC < Habitat, BOREAL < Habitat, TERRESTRIAL < Habitat, RODENTS;SHREWS < Taxon

SCHOLARONE™
Manuscripts

**Quantifying trophic niche spaces of small mammals using stable isotopes
($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) at two scales across Alaska**

A.P. Baltensperger^{*a}, F. Huettmann^b, J.C. Hagelin^c, J.M. Welker^d

^aDepartment of Biology and Wildlife, University of Alaska Fairbanks, 902 Koyukuk Dr.,
Fairbanks, Fairbanks, AK 99775, USA, abaltens@alaska.edu

^bDepartment of Biology and Wildlife, University of Alaska Fairbanks, 902 Koyukuk Dr.,
Fairbanks, AK 99775, USA, fhuettmann@alaska.edu

^cWildlife Diversity Program, Alaska Department of Fish and Game, 1300 College Rd.,
Fairbanks, AK 99701, USA, julie.hagelin@alaska.gov

^dDepartment of Biological Sciences, University of Alaska Anchorage, 3211
Providence Drive, Anchorage, AK 99508, USA, jmwelker@uaa.alaska.edu

^{*}Corresponding author: Andrew P. Baltensperger, University of Alaska Fairbanks,
902 Koyukuk Dr., Fairbanks, AK, 99775, 907-474-7959 abaltens@alaska.edu

**Quantifying trophic niche spaces of small mammals using stable isotopes
($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) at two scales across Alaska**

A.P. Baltensperger, F. Huettmann, J.C. Hagelin, J.M. Welker

Abstract

Changing climate conditions are causing global distribution shifts, resulting in altered food webs and novel species assemblages in terrestrial systems. How sympatric small mammal diets overlap and whether this may translate into competitive exclusion among new species interactions remains largely unknown. Monitoring niche overlap in changing arctic and boreal communities can assist in forecasting interspecific competition and species turnover. We quantified small mammal isotopic niche spaces, which may reflect dietary niche spaces, at study sites along two megatransects spanning Alaska. Field sampling resulted in the capture of 724 small mammals belonging to 12 species of rodent (ten Arvicolinae and two Sciuridae) and six species of shrew (*Sorex* spp.). We created dietary mixing models based on hair samples for four rodent species using stable isotope ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) analyses in R. We also modeled isotopic niche ellipses and quantified niche overlap among species at small and large scales. A varied combination of fungi and herbaceous plants composed the diets of most species. Fundamental niche spaces overlapped considerably between sympatric species statewide, but realized niche spaces were largely segregated at individual sites. We conclude that some degree of dietary plasticity served to partition niche spaces and minimize interspecific competition, allowing sympatric species to co-exist.

Key-words arctic tundra, boreal forest, community ecology, interspecific competition, mixing models, rodents, trophic position

Introduction

The fundamental ecological niche as conceptualized by Hutchinson (1957) is the space bounded by an n -dimensional hypervolume, consisting of a range of climatic and biotic variables, wherein a species is able to persist indefinitely in the absence of competition (McGill et al. 2006). At geographic scales, this concept is closely aligned with the Grinnellian notion of a species' niche being defined by its spatial distribution (Soberon 2007). Yet, biotic interactions including competition, symbiotic relationships, and predation also play important roles in outlining the portions of fundamental dietary and geographic niches that are 'realized', or occupied given the influence of other species, such that no two should occupy exactly the same space (Soberon 2007).

Outlining the realized isotopic niche spaces of species and quantifying the magnitude of interspecific niche overlap can provide a means of identifying potential competitors at local scales. The extent of isotopic overlap can aid in predicting interspecific dietary differences (Wang et al. 2004; Ercoli et al. 2014) as well as the potential for coexistence or competitive exclusion of species in new interactions (Araujo and Guisan 2006). New species interactions (e.g. between boreal and arctic species) are likely to occur at northern latitudes in the future as the warming climate pushes communities northward and upward in elevation (Williams and Jackson 2007; Murphy et al. 2010; Baltensperger and Huettmann, in press).

Theory indicates that co-occurring species compete along resource, predation, space, and time axes. Co-existence occurs because trade-offs among competitors along these axes provide each species with a unique set of advantages and disadvantages (Chesson 2000; Moll and Brown 2008). When the occupied space bounded by these axes

is similar among species, competition, and possibly exclusion will result (Chesson 2000). Determining how new species interactions will play out in this context of competition is important for predicting the consequences of shifting and overlapping wildlife distributions.

Quantifying the feeding ecology of wildlife has traditionally focused on direct observations, and fecal or stomach content analysis, but these techniques likely do not adequately reflect the quantity of nutrients assimilated into tissues and observations of cryptic species can be difficult (Gannes et al. 1998; Bearhop et al. 2004; Crawford et al. 2008). More recently, ecologists have successfully employed stable isotope analyses ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) to define the dietary niches of species and to trace nutrient flow between trophic levels and through ecosystems (Fry 2006; Layman et al. 2007a; Layman et al. 2007b; Perkins et al. 2014). Nitrogen isotopes are especially useful for differentiating between specific food sources (Phillips and Gregg 2001; Crawford et al. 2008) and assigning trophic positions to species (Post 2002; Yi et al. 2006; Anderson and Cabana 2007). Increases in $\delta^{15}\text{N}$ between 2.0‰ and 3.4‰ (Post 2002; McCutchan Jr. et al. 2003) and in $\delta^{13}\text{C}$ between 0.4‰ and 0.8‰ (Post 2002; Caut et al. 2009) with each subsequent trophic level have been documented but vary by species, tissue, and location (DeNiro and Epstein 1981; Minagawa and Wada 1984; Caut et al. 2009).

This individual variability can be employed as a measure of foraging breadth and to define the boundaries of the realized isotopic niche (Layman et al. 2007a; Jackson et al. 2011; Ercoli et al. 2014). For example, populations with high densities that consume a wide range of prey or forage species will exhibit greater variation in isotopic values, and wider niche breadths than those consuming a narrow set of dietary items (Layman et al.

2007b; Syvaranta and Jones 2008; Ercoli et al. 2014). Ultimately, patterns of co-existence may depend on limiting niche overlap between competitors at local scales, despite fundamental niche spaces that may overlap considerably at geographic scales (Ryan 1986; Hallett et al. 2003; Araujo and Guisan 2006).

In terrestrial communities of the Boreal Forest and the Arctic, rodents are important components at the base of food webs, and provide significant energy flow via predation to higher trophic level animals, including raptors and mammalian carnivorans (Robinson et al. 2014). They are also responsible for numerous ecological services and disturbances including seed dispersal (Lichti et al. 2014), symbiosis with mycorrhizal fungi (Maser et al. 1978; Luoma et al. 2003; Frank et al. 2009), soil development and fertilization (McKendrick et al. 1980; Hallett et al. 2003; Eldridge and Whitford 2009), and herbivory (Luoma et al. 2003; Gough et al. 2007; Olofsson et al. 2012). Stomach content analyses of northern rodents have shown a spectrum of dietary sources that include some combination of grasses, seeds, berries, buds, lichen, moss, fungi, and in some cases arthropods (Lensink 1983; Bangs 1984; Batzli and Henttonen 1990; Bergman and Krebs 1993; Luoma et al. 2003).

Alaska's small mammal fauna is diverse and includes 17 species of native rodents (Arvicolinae) and ten species of shrews (*Sorex* spp.). Among these, *Clethrionomys rutilus* (Pallas, 1779; northern red-backed voles; we consistently use ITIS (Integrated Taxonomic Information System) names, but see Carleton et al. 2014 for taxonomy) is one of the most common species in the boreal forest (Krebs et al. 2014) and is ubiquitous across most of the state with the exception of Arctic and coastal regions (MacDonald and Cook 2009). They are found at a range of elevations in boreal and tundra ecoregions,

inhabiting a diversity of terrestrial habitats including forests, shrublands, meadows, bogs, and talus slopes (West 1977; Zuercher et al. 1999).

As climate conditions warm, precipitation regimes change, and biomes shift northward, the distribution of *C. rutilus* (and other species; Baltensperger and Huettmann, in press) is also likely to move northward and upward in elevation, encroaching on cold-climate-adapted communities that include *Microtus oeconomus* (Pallas, 1776; root voles), *M. miurus* (Osgood, 1901; singing voles), and *Dicrostonyx groenlandicus* (Trail, 1823; collared lemmings; Gilg, Sittler and Hanski 2009; Lawler et al. 2009; Baltensperger and Huettmann, in press). The competitive outcome of these new species interactions including new species that may enter Alaska from Canada in the future (Baltensperger and Huettmann, in press) remains a significant unknown in the prediction of species persistence following climate change.

The diets of microtine rodents have been shown to contain higher proportions of grasses, sedges, and herbaceous plants than *C. rutilus*, largely due to differences in preferred habitat (Krebs et al. 2010). But the degree to which their niches overlap with *C. rutilus* and one another remains unquantified (Batzli and Jung 1980; Batzli and Henttonen 1990; Bergman and Krebs 1993). Additionally, no studies have used stable isotopes to quantify isotopic niche overlap between multiple small mammal species across broad regions.

As a tool for predicting the outcomes of new species interactions (coexistence or exclusion), we describe the fundamental and realized isotopic niches of small mammals by quantifying dietary composition, trophic breadth, and degree of niche overlap between co-occurring species at geographic and local scales across Alaska. We predict that

species with overlapping fundamental isotopic niche spaces at the statewide scale will be more partitioned in realized space at individual study sites in the presence of competitors. The degree to which small mammal isotopic niche spaces overlap with one another will help to identify the potential for interspecific dietary competition among novel small mammal interactions. Results will assist in determining the outcomes of new boreal and arctic species encounters as these occur with increasing frequency in the future.

Materials and methods

Field sampling

We trapped small mammals at 20 locations between elevations of 10m and 1132m along latitudinal and longitudinal megatransects across Alaska between 2010 and 2013 (Fig. 1). Sampling sites were located in a diversity of habitats and ecoregions across the state. Most low-elevation sites were dominated by *Picea mariana* (Mill.; black spruce) forests, interspersed with ericaceous shrubs and *Sphagnum* spp. (peat-moss) wetlands. Mid-elevation sites were comprised of a mixture of *P. glauca* ((Moench) Voss; Fig. 1) and black spruce, as well as mixed hardwoods, ericaceous shrubs and *Salix* spp. (willows). High elevation sites and the two northernmost sites were devoid of trees and dominated by ericaceous shrubs and graminoid (e.g., *Carex* spp., *Eriophorum* spp.) tussock tundra.

At each site we placed 300 traps (200 Sherman live-traps (7.6 x 8.9 x 22.9 cm), 50 Museum Special snap traps (7 x 14 cm), and 50 pitfall traps (d=10.2 cm, h=17.8 cm)) throughout the range of available habitats along three 1-km trapping loops emanating from the plot center. Traps were checked twice daily and remained open for five days and nights. Locations of captured individuals were recorded using a Garmin GPS and

specimens were measured, processed, and preserved for archival at the University of Alaska Museum of the North.

Isotope analysis

Hair samples from 329 small mammals belonging to 17 species of rodent and shrew were collected. Hair was sampled by shaving a 1-cm² patch of hair from the rump and preserved dry in a paper coin envelopes. Hair samples were cleaned using a 2:1 methanol/chloroform solution, dried in a Blue-M #OV-18A oven (Thermal Product Solutions, White Deer, PA, USA), and homogenized in a 6770 Freezer/Mill (Spex Sampleprep, Matuchen, NJ, USA). Available food sources of rodents were sampled opportunistically from among the dominant species available. Three to five samples from each of five vegetative groups (herbaceous plants, woody plants, lichens, mosses, and fungi) were collected from each site. Vegetation samples were stored dry in paper envelopes before being ground and homogenized in a BeadbeaterMini with 3.2 mm chrome/steel beads (Biospec Products, Inc., Bartlesville, OK, USA).

Approximately 300–800 µg of hair and vegetation were weighed into tin capsules, combusted, and analyzed for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ on a continuous flow mass spectrometry system at the University of Alaska Anchorage Stable Isotope Laboratory. The isotopic ratios were reported in units per thousand (‰) against the international standards of Vienna Pee Dee Belemnite for carbon and AIR for nitrogen. Internal standards (BWBII keratin, peach leaves, moose (Linnaeus, 1758; *Alces alces*), and three-spined stickleback (Linnaeus, 1758; *Gasterosteus aculeatus*) were used to determine an accuracy of $\pm 1 \sigma = 0.3\text{‰}$ for both carbon and nitrogen.

Because rodents moult in a series of continuous waves over their body, it can be difficult to determine exactly when hair was grown and thus the time period for which isotope samples are representative of diet (Sare et al. 2005a). Adult voles generally molt once in early spring (late April or early May; Al-Khateeb and Johnson 1971), and in Alaska tend to grow their summer pelage during the month of May (Sealander 1979). They do not moult again until autumn (late September or early October), and so any hair collected during the summer should be representative of their spring diet during late April and May (Sealander 1979). Because of caching of fungi, seeds, and berries (Krebs et al. 2010), spring diet may include over-winter stores that were collected during the previous autumn.

Trophic niche analysis

We used the stable isotope analysis package in R (SIAR; (Parnell et al. 2010) in R2.12.1 (R Core Team 2013) to create five-source mixing models using $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for hair samples belonging to four rodent species at 17 of the 20 sites with sufficient sample sizes. Samples were pooled across study sites where species occurred before being analyzed. SIAR uses a Bayesian process to calculate all possible solutions to the model and provides the most likely range of solutions (95% credible intervals) among potential dietary proportions (Parnell et al. 2010; Table 1). This type of model is considered to be an improvement over previous mixing models (e.g., linear mixing models or IsoSource; Phillips and Gregg 2001) in that it incorporates sources of uncertainty into posterior probability distributions of consumer and source isotopic values (Parnell et al. 2010; Ercoli et al. 2014). Models yielded the most probable proportions of

diet based on mean and standard deviations of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of each consumer, five dietary sources, and trophic enrichment factors. Mean and standard deviation of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ were calculated for consumers and vegetation functional groups and used as source inputs to SIAR. The most appropriate mean diet-to-tissue trophic enrichment priors input to SIAR were selected from the literature: 2.7‰ ($\sigma = 1.67$) for $\delta^{15}\text{N}$ and 2.4‰ ($\sigma = 1.01$) for $\delta^{13}\text{C}$ (Parnell et al. 2010; Sare et al. 2005b). Datasets met model-assumptions for normal distributions and we used a non-informative dirichlet prior for source contribution. Samples for rodent consumers and vegetation sources were pooled by species across study sites where taxa were present. Models were not constructed for other rodents because of insufficient sample sizes ($n < 4$) or shrews because invertebrate prey were not sampled.

Isotopic niche space was quantified for eight rodents using the Stable Isotope Bayesian Ellipse package in R (SIBER; Table 1). SIBER was used to plot species niche ellipses and convex hulls, and to quantify niche overlap between species at study-site and statewide scales (Jackson et al. 2011). Unlike convex hulls (Layman et al. 2007a), which are sensitive to sample size, ellipses generated by SIBER are unbiased with respect to sample size, allowing for more robust comparisons among communities (Jackson et al. 2011). The statewide analysis was pooled across all study sites and did not account for interspecific interactions, thus reflecting species' fundamental niche spaces, while study-site analyses were more reflective of realized patterns in niche occupancy. We adjusted $\delta^{15}\text{N}$ values to trophic position to account for site-to-site variations in baselines using the formula: $Tp = 1 + (\delta^{15}\text{N}_{\text{rodent}} - \delta^{15}\text{N}_{\text{baseline}})/\Delta n$, where Tp = continuous trophic position, and Δn = trophic fractionation between the consumer and the base, in this case 2.7‰

(Post 2002; Anderson and Cabana 2007). Herbaceous plants were used as the primary producer to represent the first order baseline because all species consumed them, they were present at all sites, and variation was low across Alaska (Anderson and Cabana 2007; Ercoli et al. 2014). $\Delta^{13}\text{C}_{\text{rodent}}$ values were also corrected to account for differences in baselines using $\delta^{13}\text{C}_{\text{c}} = (\delta^{13}\text{C}_{\text{rodent}} - \delta^{13}\text{C}_{\text{baseline}}) / \delta^{13}\text{C}_{\text{baseline}}$, where $\delta^{13}\text{C}_{\text{c}}$ was the corrected $\delta^{13}\text{C}$ value and herbaceous plants were used as the baseline (Ercoli et al. 2014). Trophic position was used to infer relative levels of omnivory (Anderson and Cabana 2007), and together with $\delta^{13}\text{C}_{\text{c}}$ these metrics composed the isotopic dimensions of species dietary niche space.

Statewide and site-specific core niche areas were calculated for each species based on an ellipse of one standard deviation centered on the mean, containing roughly 40% of the data (Jackson et al. 2011; Ercoli et al. 2014). Convex hulls included the full extent of the data and were included to delineate the full range of samples. We used SIBER to calculate the area of ellipse overlap between co-occurring species at both study-site and statewide scales. Areas of overlap were divided by the sum of ellipse areas for co-occurring species to determine the percentage of niche overlap between species (0–50%).

Results

Isotopic niche space of taxa

Over a period of 30,700 trap-nights, 724 small mammals belonging to 17 species of rodent and six species of shrew were captured at 20 locations across Alaska (Table 1). Stable isotope values varied among sites and ranged between -0.14‰ and 7.44‰ for

$\delta^{15}\text{N}_{\text{hair}}$ and between -31.5‰ and -21.5‰ for $\delta^{13}\text{C}_{\text{hair}}$ (Table S1). After correcting isotope values to account for differences in baselines, mean trophic position calculations ranged between 0.7 for *D. groenlandicus* and 2.8 for *M. pennsylvanicus* (Ord, 1815; meadow voles; Table 2). Plotted in dual isotope space, trophically adjusted stable isotope means and 95% confidence intervals placed the pooled isotopic niche space of rodents between the regions occupied by fungi and herbaceous plants (Fig. 2). Shrew $\delta^{15}\text{N}$ was 2.1‰ greater and $\delta^{13}\text{C}$ was 0.9‰ greater than rodents. The trophically-adjusted isotopic space of shrews was closest to fungi, although invertebrates were not sampled (Fig. 2).

Dietary composition of rodents

Patterns in dietary composition calculated by mixing models varied extensively in the proportions and combinations of dietary sources preferred by rodents (Fig. 3). Herbaceous plants comprised the largest proportions of all diets with the exception of *D. groenlandicus*. The proportion of herbaceous plants was largest for *M. oeconomus* (0.52), which was the only diet with proportions of fungi significantly less than herbaceous plants. *Clethrionomys rutilus* consumed more fungi (0.37) than the other three species, and also consumed the smallest average amount of lichen (0.02) and woody plants (0.03). The average diets of *D. groenlandicus* and *M. miurus* were the most diverse and were comprised more of woody plants, mosses, and lichens than other species. Models for *C. rutilus* and *M. oeconomus* differentiated well between sources, with the exception of herbaceous and fungi in *C. rutilus*. Other models had more difficulty differentiating between herbaceous plants, woody plants, and moss and as such credible intervals were large in many cases.

Niche overlap

Stable isotopes ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) varied substantially both among study-sites for a given species and among species at the same location (Table S1). Averaged across populations, a clear pattern of the consumption of sources with high $\delta^{15}\text{N}$ values was evident for *C. rutilus*, *M. oeconomus*, *M. miurus*, and *M. pennsylvanicus* (Table 2, Fig. 4). This is contrasted by the lower $\delta^{15}\text{N}$ values of *D. groenlandicus*, *M. longicaudus* (Merriam, 1888; long-tailed voles), and *M. xanthognathus* (Leach 1815; yellow-cheeked vole; Table 2, Fig. 4). $\delta^{15}\text{N}$ values varied extensively among sites from *D. groenlandicus* at the Canning River (0.6‰) to *C. rutilus* at Fox Point Island (4.3‰; Table 2, Fig. 4). The highest $\delta^{15}\text{N}$ value (7.1‰) occurred at Yukon Crossing in both *C. rutilus* and *M. oeconomus* (Table 2).

Plotted against trophic position, $\delta^{13}\text{C}$ added a second dimension for defining isotopic niche position and extent (Fig. 4). Most species demonstrated extensive overlap with sympatric species in their statewide fundamental niche ellipses. The *C. rutilus* ellipse overlapped substantially with that of *M. oeconomus* (29.7%), while overlap with other co-occurring species ranged from 0% to 17.2%. Trophic positions of *M. oeconomus* were elevated and similar to *C. rutilus*, but the former had slightly lower $\delta^{13}\text{C}$. *Microtus miurus* and *M. pennsylvanicus* occupied similarly high trophic positions and their niche spaces overlapped with *M. oeconomus* by 15.6% and 14.0%, respectively. *Dicrostonyx groenlandicus* occupied a low trophic position but also a space high in $\delta^{13}\text{C}$, whereas *Synaptomys borealis* (Richardson, 1828; northern bog-lemmings) trophic positions were highly variable and their $\delta^{13}\text{C}$ values were the lowest of any species. These were also the

only two species whose niche ellipses did not overlap with any others (Fig. 4). Niche ellipses of *M. xanthognathus* overlapped with those of *M. oeconomus* (8.8%), *M. pennsylvanicus* (8.7%), and *M. miurus* (8.6%), while *M. longicaudus* and *M. xanthognathus* intersected only slightly (5.1%)

Realized niche ellipses were more segregated from one another in isotopic space across Alaska; overlap occurred between the niche spaces of co-occurring species at three of the eight sites (where $n > 3$ individuals per species; Fig. 5). The best example of niche segregation occurred at the biodiverse White Mountains site, where three species coexisted without any core intersection (Fig. 5h). The most significant overlap at the study-site scale occurred between *C. rutilus* and *M. miurus* at Isabel Pass, where 13.7% of the total niche area was occupied by both species (Fig. 5c). The other two intersections occurred between *C. rutilus* and *M. oeconomus* at Chandalar River (11.6%; Fig. 5b) and Kenai Lowlands (10.8%; Fig. 5d).

Discussion

Alaskan small mammals differed somewhat in the proportions of fungi and herbaceous plants they consumed (Fig. 3), resulting in fine-scale partitioning of niche spaces at the site scale (Fig. 5). However, isotopic analyses indicated extensive fundamental niche overlap between species at the regional scale (Fig. 4). These results point to plasticity in the realized dietary niche spaces of small mammals (Soininen et al. 2014). This flexibility may act to preclude extensive competition between species, even as new community assemblages develop as a consequence of shifting species distributions resulting from climate change (McGill et al. 2006).

Dietary composition by species

Variations in proportions of fungi consumed versus herbaceous plants largely account for differences in trophic position and niche differentiation between species. *Clethrionomys rutilus* incorporated the highest percentage of fungi into their diets compared to all other species. Stomach content analyses have also shown them to consume large amounts of mycorrhizal fungi (Maser et al. 1978; Luoma et al. 2003). Disproportionate uptake of an enriched food source like fungi would explain their elevated trophic position and high $\delta^{13}\text{C}$. Specialization on fungi could be one mechanism allowing them to minimize dietary overlap and interspecific competition with *Microtus* spp., at least when fungi are available in the fall or present in overwinter caches.

Elevated trophic position may also be an indication of omnivory (Post 2002, Anderson and Cabana 2007), and unanalyzed sources such as invertebrates, bird eggs, or carrion could have contributed to their higher niche position as well (Sealy 1982; Batzli 1985). Additionally, because of low nitrogen concentrations in berries (Phillips and Koch 2002), woody plants may be underrepresented in species like *C. rutilus* that consume berries, but not leaf or stem material (Krebs et al. 2010), as is more common for *D. groenlandicus* or *M. miurus* (Rodgers and Lewis 1986; Bergman and Krebs 1993; Fig. 2).

Herbaceous plants were also an important dietary component for all species, and their proportion was highest in *M. oeconomus*. Although they also consumed fungi, their low ratio of fungi-to-herbaceous consumption differentiated them along this axis from *C. rutilus*. Habitat partitioning between these species as well as the availability of different foods was observed as possible mechanisms for avoiding competition for among species

(Soininen et al. 2015). This is supported by stomach-content analyses, which found that *M. oeconomus* typically consume more herbaceous material (monocots) than *C. rutilus* (Bangs 1984; MacDonald and Cook 2009).

The fundamental dietary niche position of *M. miurus* also overlapped substantially with that of *M. oeconomus*. Similar to *M. oeconomus*, mixing models for *M. miurus* also indicated herbaceous plants to be marginally more important in their diet than fungi (Fig. 3). This is consistent with foraging studies conducted in Alaska which found that while both species primarily consumed herbaceous plants, *M. miurus* were partial to dicots (especially *Equisetum* spp.) and *M. oeconomus* preferred monocots like *Eriophorum* spp. (cottongrass) and *Carex* spp. (true sedges; Batzli and Henttonen 1990).

Dicrostonyx groenlandicus showed similar dietary patterns to *M. miurus* yet they occupied very different isotopic niche positions. Mixing models found that they consumed relatively high proportions of woody plants, mosses, and herbaceous plants during the winter. These results largely concur with prior diet analyses that showed *D. groenlandicus* to consume primarily dicots including *Dryas integrifolia* (entireleaf mountain-avens; Vahl) and *Salix arctica* (arctic willow; Pall) in summer (Batzli and Jung 1980; Rodgers and Lewis 1986; Bergman and Krebs 1993). The higher proportional consumption of food sources with lower isotope values (e.g. woody plants and mosses), and low consumption of fungi and herbaceous plants by *D. groenlandicus* may be an explanation for its low trophic position and differentiated niche space.

Interspecific Niche Competition

Isotopic niche spaces varied for each species among sites, demonstrating the shifting nature of the realized dietary niche (Fig. 5) versus the more stable fundamental niche (Fig. 4). The combination of intersecting dietary niches at the statewide scale, broad spatial variation, and a lack of realized niche overlap at most study sites suggests that species may be capable of adjusting their diets or preferred habitats locally in order to minimize foraging competition with sympatric species (Holt 1993; Soininen et al. 2013). This is consistent with what niche theory predicts for communities that compete for limited resources. When sympatric species are limited by a single resource, niche partitioning cannot occur, but where multiple resources or predators exist, local niche partitioning is possible (Amarasekare 2008). Additionally, smaller-bodied species (e.g., *C. rutilus*) that may consistently lose aggressive encounters over one resource (e.g., herbaceous plants) to larger-bodied species (e.g. *M. oeconomus*; Grant 1972; McGill et al. 2006) can find stabilizing advantage in another resource (e.g., fungi) allowing for co-existence.

The broad intersection of fundamental trophic niche space between *M. oeconomus* and *C. rutilus* indicates significant potential for strong competition between these species where they co-occur. Because of the coarseness of the dietary source groups, it is still possible that further dietary segregation may be occurring at finer scales (e.g., within taxonomic Family) than our models were able to detect. Nevertheless, the dietary niche comprises only a single axis of the overall fundamental niche of a species, and other spatial and environmental constraints including variations in habitat and range extents must also be considered when quantifying the fundamental niche breadth species. Analyses of the geographic overlap between species have indicated that distributions of

M. miurus, *M. oeconomus*, and *D. groenlandicus* were correlated with one another, as were *C. rutilus* with *M. xanthognathus*, and *M. pennsylvanicus* with *S. borealis* (Baltensperger and Huettmann 2015). The dietary preferences of *D. groenlandicus* and *S. borealis* appear to be specialized enough to avoid competition with both similarly distributed specialist and generalist species (Morris 1996). In other cases even though fundamental dietary niches may overlap (e.g., *M. pennsylvanicus* and *M. oeconomus*), because species do not have sympatric distributions, competition is avoided. While all distributions overlap to some degree (especially with *C. rutilus*), the only species combination with both highly correlated distributions and similar fundamental isotopic niche spaces are *M. oeconomus* and *M. miurus*.

When *M. miurus* or *M. oeconomus* co-occur with *C. rutilus* (e.g., Figs 5b, c, d), realized niches overlap and competition for limited resources could exist. However, Batzli and Henttonen (1990) showed a finer preference for dicots and monocots, by these respective species. In this analysis, these sources were pooled together as a single functional group and so no distinction in consumption could be made. Our results show that *M. oeconomus* may also be more dependent on herbaceous plants than mosses, whereas these proportions are roughly equal in *M. miurus*. These dietary differences may be one mechanism for differentiating foraging habits between these species and thus for avoiding interspecific competition. A separation of preferred habitats has also been observed between these species, pointing to fine-scale spatial partitioning even in regions where they co-occur (Galindo and Krebs 1985; Batzli and Henttonen 1990).

Implications of Climate Change

As climate change acts to rearrange species distributions and community assemblages, the number of species combinations sharing similar dietary and geographic niche spaces may change (McGill et al. 2006; Williams and Jackson 2007).

Clethrionomys rutilus, whose niche space currently overlaps those of *M. oeconomus*, *M. pennsylvanicus*, and *M. miurus*, are predicted to expand northward and upward in elevation (Williams and Jackson 2007; Baltensperger and Huettmann, in press). If future distributions result in more frequent contact between these four species, even small intersections in their diets could lead to increased dietary competition and exclusion near niche boundaries where competitive disadvantages cannot be offset along other niche axes. As an example, Bergman and Krebs (1993) concluded that dietary competition was minimal between wild *D. groenlandicus* and *M. oeconomus*, but that overlap increased when the two species were forced to select between a limited set of available plants.

In contrast, the isolation of the fundamental dietary niche of *D. groenlandicus* and *S. borealis* (Fig. 4) may serve to insulate them from competition with *C. rutilus* and other voles as the distributions of boreal species encroach into the Arctic. Whether *D. groenlandicus* can persist in the context of expanding boreal species will not only depend on interspecific competition, but also whether changes in tundra vegetation can adequately provide for the nutritional needs of healthy populations (Rose and Birney 1980). As tundra vegetation (*Dryas* spp. and *Carex* spp.) gives way to encroaching shrubs from the south (Tape et al. 2012), it is uncertain whether arctic and alpine species will be able to adapt to these changing conditions. Recent investigations, however, have documented the frequent consumption of *Salix* spp. by lemmings, especially in snowbeds (Soininen et al. 2015), which are conducive to shrub recruitment in a greening Arctic

(Tape et al. 2012, Cable et al. 2014). If arctic species are able to adapt to this changing system, they may do so by exploiting abundant resources, but they will also likely encounter heightened competition from a host of vole species that have already established their own niches within the encroaching boreal habitats. Ultimately the composition of these new communities will depend on the degree of niche plasticity among competitors and the availability of unoccupied niche space.

Acknowledgements

Thank you to everyone who helped collect data in the field, especially D. Keiter, E. Corp, J. Jordan, A. Nicely, C. Brown, T. Mullet, L. Kövér, and D. Korobitsyn. The authors are also grateful to M. Rogers, N. Bargmann, and L. Miller for processing samples for stable isotope analyses at the University of Alaska Anchorage Stable Isotope Facility established by JMW and funded in part by a NSF MRI award (0923571). We are indebted to the Mammals Lab at the University of Alaska Museum of the North, especially Link Olson for lending traps and supplies and to Rachel Noriega for processing specimens. Thank you to Colin Tucker and Sasha Kitaysky for interesting and valuable discussions. FH and JMW helped to conceive and design the project and provided editing assistance. JCH made valuable written contributions to the manuscript. Permission to trap and collect small mammals was obtained from the International Animal Care and Use Committee (#172650) and from the Alaska Department of Fish and Game (ADF&G; #10-135). Funding was provided by the Calvin J. Lensink Graduate Fellowship in Wildlife Biology, the Ted McHenry Biology Field Research Scholarship, and the Alaska Department of Fish and Game Wildlife Diversity Program.

References

- Al-Khateeb, A., and Johnson, E. 1971. Seasonal changes of pelage in the vole (*Microtus agrestis*). Gen. Comp. Endocrinol. **16**: 217-228.
- Amarasekare, P. 2008. Spatial dynamics of foodwebs. Annu. Rev. Ecol. Evol. Syst. **39**: 479-500.
- Anderson, C., and Cabana, G. 2007. Estimating the trophic position of aquatic consumers in river food webs using stable nitrogen isotopes. J. N. Am. Benthol. Soc. **26**(2): 227-285.
- Araujo, M.B., and Guisan, A. 2006. Five (or so) challenges for species distribution modelling. J. Biogeogr. **33**(10): 1677-1688. doi: 10.1111/j.1365-2699.2006.01584.x.
- Baltensperger, A.P. and Huettmann, F. In press. Predicted shifts in small mammal distributions and biodiversity in the altered future environment of Alaska: An open access data and machine learning perspective. PLoS One.
- Baltensperger, A.P., and Huettmann, F. 2015. Predictive spatial niche and biodiversity hotspot models for small mammal communities in Alaska: Applying machine-learning to conservation planning. Land. Ecol. **30**: 681-697.
- Bangs, E.E. 1984. Summer food habits of voles, *Clethrionomys rutilus* and *Microtus pennsylvanicus*, on the Kenai Peninsula, Alaska. Can. Field-Nat. **98**(4): 489-492.
- Batzli, G.O. 1985. Nutrition. In Biology of new world *Microtus*. Edited by R.H. Tamarin. American Society of Mammalogists, Boston. pp. 779-811.
- Batzli, G.O., and Henttonen, H. 1990. Demography and resource use by Microtine rodents near Toolik Lake, Alaska, USA. Arct. Alp. Res. **22**(1): 51-64.

- Batzli, G.O., and Jung, H.G. 1980. Nutritional ecology of microtine rodents: resource utilization near Atkasook, Alaska. *Arct. Alp. Res.* **12**: 483-499.
- Bearhop, S., Adams, C.E., Waldron, S., Fuller, R.A., and MacLeod, H. 2004. Determining trophic niche width: a novel approach using stable isotope analysis. *J. Anim. Ecol.* **73**: 1007-1012.
- Bergman, C.M., and Krebs, C.J. 1993. Diet overlap of collared lemmings and tundra voles at Pearce Point, Northwest Territories. *Can. J. Zoo.* **71**: 1703-1709.
- Cable, J.M., Ogle, K., Bolton, W.R., Bentley, L.P., Romanovsky, V., Iwata, H., Harazono, Y., and Welker, J. 2014. Permafrost thaw affects boreal deciduous plant transpiration through increased soil water, deeper thaw, and warmer soils. *Ecohydrology* **7**(3): 982-997. doi: 10.1002/eco.1423.
- Carleton, M.D., Gardner, A.L., Pavlinov, I.Y., and Musser, G.G. 2014. The valid generic name for red-backed voles (Muroidea: Cricetidae: Arvicolinae): restatement of the case for *Myodes* Pallas, 1811. *J. Mammal.* **95**: 943-959.
- Caut, S., Angulo, E., and Courchamp, F. 2009. Variation in discrimination factors ($\Delta N-15$ and $\Delta C-13$): the effect of diet isotopic values and applications for diet reconstruction. *J. Appl. Ecol.* **46**(2): 443-453. doi: 10.1111/j.1365-2664.2009.01620.x.
- Chesson, P. 2000. Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.* **31**: 343-366. doi: 10.1146/annurev.ecolsys.31.1.343.
- Crawford, K., McDonald, R.A., and Bearhop, S. 2008. Applications of stable isotope techniques to the ecology of mammals. *Mamm. Rev.* **38**: 87-107.

- DeNiro, M.J., and Epstein, S. 1981. Influence of diet on the distribution of nitrogen isotopes in animals. *Geochim. Cosmochim. Acta*, **45**: 341-351.
- Eldridge, D.J., and Whitford, W.G. 2009. Soil disturbance by native animals along grazing gradients in an arid grassland. *J. Arid Environ.* **73**(12): 1144-1148. doi: 10.1016/j.jaridenv.2009.06.005.
- Ercoli, F., Ruokonen, T.J., Hämäläinen, H., and Jones, R. 2014. Does the introduced signal crayfish occupy an equivalent trophic niche to the lost native noble crayfish in boreal lakes? *Biol. Invasions*, **16**: 2025-2036.
- Frank, J.L., Anglin, S., Carrington, E.M., Taylor, D.S., Viratos, B., and Southworth, D. 2009. Rodent dispersal of fungal spores promotes seedling establishment away from mycorrhizal networks on *Quercus garryana*. *Botany-Botanique*, **87**(9): 821-829.
- Fry, B. 2006. *Stable Isotopes in Ecology*. Springer, New York, NY, USA.
- Galindo, C., and Krebs, C.J. 1985. Habitat use by singing voles and tundra voles in the southern Yukon. *Oecologia*, **66**(3): 430-436. doi: 10.1007/bf00378311.
- Gannes, L.Z., Rio, C.M.d., and Koch, P. 1998. Natural abundance variations in stable isotopes and their potential uses in animal physiological ecology. *Compositions in Biochem. Physiol.* **119A**(3): 725-737.
- Gilg, O., Sittler, B., and Hanski, I. 2009. Climate change and cyclic predator-prey population dynamics in the high Arctic. *Global Change Biol.* **15**: 2634-2652.
- 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.

- Grant, P.R. 1972. Interspecific competition among rodents. *Annu. Rev. Ecol. Syst.* **3**: 79-106.
- Hallett, J., O'Connell, M., and Maguire, C. 2003. Ecological relationships of terrestrial small mammals in western coniferous forests. *In* Mammal community dynamics: management and conservation in the coniferous forests of western North America. *Edited by* C.J. Zabel and R.G. Anthony. Cambridge University Press, New York. p. 22.
- Holt, R.D. 1993. Ecology at the Mesoscale: The influence of regional processes on local communities. *In* Species Diversity: Historical and Geographical Perspectives. *Edited by* Ricklefs and Schluter. University of Chicago Press, Chicago. pp. 77-88.
- Huettmann, F., and Gottschalk, T. 2010. Simplicity, model fit, complexity and uncertainty in spatial prediction models applied over time: We are quite sure, aren't we? *In* Predictive species and habitat modeling in landscape ecology. *Edited by* C.A. Drew, Yolanda F. Wiersma, Falk Huettmann. Springer Science Business Media, LLC, Berlin. pp. 189-208.
- Hutchinson, G.E. 1957. Concluding remarks. Cold Spring Harbour Symposium on Quantitative Biology, **22**: 415-427.
- Jackson, A.L., Parnell, A.C., Inger, R., and Bearhop, S. 2011. Comparing isotopic niche widths among and within communities: SIBER-Stable Isotope Bayesian Ellipses in R. *J. Anim. Ecol.* **80**: 595-602.
- Krebs, C.J., Boonstra, R., Boutin, S., Sinclair, A.R.E., Smith, J.N.M., Gilbert, B.S., Martin, K., O'Donoghue, M., and Turkington, R. 2014. Trophic dynamics of the boreal forests of the Kluane Region. *Arctic*, **67**: 71-81.

- Krebs, C.J., Cowcill, K., Boonstra, R., and Kenney, A.J. 2010. Do changes in berry crops drive population fluctuations in small rodents in the southwestern Yukon? *J. Mammal.* **91**(2): 500-509. doi: 10.1644/09-mamm-a-005.1.
- Lawler, J.J., Shafer, S.L., White, D., Kareiva, P., Maurer, E.P., Blaustein, A.R., and Bartlein, P.J. 2009. Projected climate-induced faunal change in the Western Hemisphere. *Ecology*, **90**: 588-597.
- Layman, C.A., Arrington, D.A., Montana, C.G., and Post, D.M. 2007a. Can stable isotope ratios provide for community-wide measures of trophic structure? *Ecology*, **88**(1): 42-48. doi: 10.1890/0012-9658(2007)88[42:csirpf]2.0.co;2.
- Layman, C.A., Quattrochi, J.P., Peyer, C.M., and Allgeier, J.E. 2007b. Niche width collapse in a resilient top predator following ecosystem fragmentation. *Ecol. Lett.* **10**: 937-944.
- Lensink, C.J. 1983. Occurrence of *Microtus xanthognathus* in Alaska. *J. Mammal.* **35**: 259-260.
- Lichti, N.I., Steele, M.A., Zhang, H., and Swihart, R.K. 2014. Mast species composition alters seed fate in North American rodent-dispersed hardwoods. *Ecology*, **95**(7): 1746-1758.
- Luoma, D.L., Trappe, J.M., Claridge, A.W., Jacobs, K.M., and Cazares, E. 2003. Relationships among fungi and small mammals in forested ecosystems. *In* Mammal community dynamics. Management and conservation in the coniferous forests of Western North America. *Edited by* Z.C. J. and R.G. Anthony. Cambridge University Press, Cambridge, UK. pp. 343-373.

- MacDonald, S.O., and Cook, J.A. 2009. Recent Mammals of Alaska. University of Alaska Press, Fairbanks. pp. xii - 387.
- Maser, C., Trappe, J.M., and Nussbaum, R. 1978. Fungal-small mammal interrelationships with emphasis on Oregon coniferous forests. *Ecology*, **59**(4): 799-809.
- McCutchan Jr., J.H., Jr., W.M.L., Kendall, C., and McGrath, C.C. 2003. Variation in trophic shift for stable isotope ratios of carbon, nitrogen and sulfur. *Oikos*, **102**(2): 378-390.
- McGill, B.J., Enquist, B.J., Weiher, E., and Westoby, M. 2006. Rebuilding community ecology from functional traits. *Trends Ecol. Evol.* **21**(4): 178-185. doi: 10.1016/j.tree.2006.02.002.
- McKendrick, J.D., Batzli, G.O., Everett, K.R., and Swanson, J.C. 1980. Some effects of mammalian herbivores and fertilization on tundra soils and vegetation. *Arct. Alp. Res.* **12**(4): 565-578.
- Minagawa, M., and Wada, E. 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between $\delta^{15}\text{N}$ and animal age. *Geochim. Cosmochim. Acta*, **48**: 1135-1140.
- Moll, J.D., and Brown, J.S. 2008. Competition and coexistence with multiple life-history stages. *Am. Nat.* **171**(6): 839-843. doi: 10.1086/587517.
- Morris, D.W. 1996. Coexistence of specialist and generalist rodents via habitat selection. *Ecology*, **77**: 2352-2364.
- Murphy, K., Huettmann, F., Fresco, N., and Morton, J. 2010. Connecting Alaska landscapes into the future: Results from an interagency climate modeling, land

- management and conservation project. Final Report, U.S. Fish and Wildlife Service, Fairbanks, AK.
- Olofsson, J., Tommervik, H., and Callaghan, T.V. 2012. Vole and lemming activity observed from space. *Nature Climate Change* **2**: 880-883.
- Parnell, A.C., Inger, R., Bearhop, S., and Jackson, A.L. 2010. Source partitioning using stable isotopes: Coping with too much variation. *PLoS ONE* **5**(3): 1-5.
- Perkins, M.J., McDonald, R.A., van Veen, F.J.F., Kelly, S.D., Rees, G., and Bearhop, S. 2014. Application of nitrogen and carbon stable isotopes (δ N-15 and δ C-13) to quantify food chain length and trophic structure. *PLoS ONE* **9**(3): 1-10.
- Phillips, D.L., and Gregg, J.W. 2001. Uncertainty in source partitioning using stable isotopes. *Oecologia*, **127**(2): 171-179. doi: 10.1007/s004420000578.
- Phillips, D.L., and Koch, P.L. 2002. Incorporating concentration dependence in stable isotope mixing models. *Oecologia*, **130**(1): 114-125. doi: 10.1007/s004420100786.
- Post, D.M. 2002. Using stable isotopes to estimate trophic position: Models, methods, and assumptions. *Ecology*, **83**(3): 703-718.
- Robinson, B.G., Franke, A., and Derocher, A.E. 2014. The influence of weather and lemmings on spatiotemporal variation in the abundance of multiple avian guilds in the Arctic. *PLoS ONE* **9**(7): 1-11.
- Rodgers, A.R., and Lewis, M.C. 1986. Diet selection in Arctic lemmings (*Lemmus sibiricus* and *Dicrostonyx groenlandicus*): forage availability and natural diets. *Can. J. Zool.* **64**: 1684-1689.

- Rose, R.K., and Birney, E.C. 1980. Community Ecology. *In* Biology of New World *Microtus*. Edited by R.H. Tamarin. The American Society of Mammalogists, Boston, MA, USA. pp. 310-335.
- Ryan, J.M. 1986. Dietary overlap in sympatric populations of pygmy shrews, *Sorex hoyi*, and masked shrews, *Sorex cinereus*, in Michigan. *Can. Field-Nat.* **100**: 225-228.
- Sare, D.T.J., Millar, J.S., and Longstaffe, F.J. 2005a. Moulting patterns in *Clethrionomys gapperi*. *Acta Theriologica* **50**: 561-569.
- Sare, D.T.J., Millar, J.S., and Longstaffe, F.J. 2005b. Tracing dietary protein in red-backed voles (*Clethrionomys gapperi*) using stable isotopes of nitrogen and carbon. *Can. J. Zool.* **83**: 717-725.
- Sealand, J.A. 1979. Circum-annual changes in age, pelage characteristics and adipose tissue in the Northern red-backed vole. *Acta Theriologica*, **17**(1): 1-24.
- Sealy, S.G. 1982. Voles as a source of egg and nestling loss among nesting auklets. *Murrelet*, **63**: 9-14.
- Soberon, J. 2007. Grinnellian and Eltonian niches and geographic distributions of species. *Ecol. Lett.* **10**(12): 1115-1123. doi: 10.1111/j.1461-0248.2007.01107.x.
- Soininen, E.M., Ehrlich, D., Lecomte, N., Yoccoz, N.G., Tarrux, A., Berteaux, D., Gauthier, G., Gielly, L., Brochmann, C., Gussarova, G., and Ims, R.A. 2014. Sources of variation in small rodent trophic niche: new insights from DNA metabarcoding and stable isotope analysis. *Isotopes Environ. Health Stud.* **50**: 361-381.
- Soininen, E.M., Gauthier, G., Bilodeau, F., Berteaux, D., Gielly, L., Taberlet, P., Gussarova, G., Bellemain, E., Hassel, K., Stenoien, H.K., Epp, L.S., Schröder-

- Nielsen, A., Brochmann, C., and Yoccoz, N.G. 2015. Highly overlapping winter diet in two sympatric lemming species revealed by DNA metabarcoding. *PLoS ONE* **10**. doi: 10.1371/journal.pone.0115335.
- Soininen, E.M., Ravolainen, V., Brathen, K.A., Yoccoz, N.G., Gielly, L., and Ims, R.A. 2013. Arctic small rodents have diverse diets and flexible food selection. *PLoS ONE*, **8**: 1-13.
- Syvaranta, J., and Jones, R.I. 2008. Changes in feeding niche widths of perch and roach following biomanipulation, revealed by stable isotope analysis. *Freshwat. Biol.* **53**(3): 425-434. doi: 10.1111/j.1365-2427.2007.01905.x.
- Tape, K.D., Hallinger, M., Welker, J.M., and Ruess, R.W. 2012. Landscape heterogeneity of shrub expansion in Arctic Alaska. *Ecosystems*, **15**: 711-724.
- Wang, J., Lin, G., Huang, J., and Han, X. 2004. Applications of stable isotopes to study plant-animal relationships in terrestrial ecosystems. *Chin. Sci. Bull.* **49**(22): 2239-2347.
- West, S. 1977. Midwinter aggregation in the northern red-backed vole, *Clethrionomys rutilus*. *Can. J. Zool.* **55**: 1504-1409.
- Williams, J.W., and Jackson, S.T. 2007. Novel climates, no-analog communities, and ecological surprises. *Front. Ecol. Environ.* **5**(9): 475-482.
- Yi, X., Yang, Y., and Zhang, X. 2006. Modeling trophic positions of the alpine meadow ecosystem combining stable carbon and nitrogen isotope ratios. *Ecological Modeling*, **193**: 801-808.

Zuercher, G.D., Roby, D., and Rexstad, E. 1999. Seasonal changes in body mass, composition, and organs of northern red-backed voles in Interior Alaska. *J. Mammal.* **80**(2): 443-459.

Draft

Tables

Table 1. Integrated Taxonomic Information System (ITIS)-derived scientific names, common names, and Taxonomic Serial Numbers (TSN) for species. Full list includes all species captured during field sampling, * denotes species for which niche ellipses were calculated, and † denotes species for which dietary mixing models were created.

Species	Common Name	TSN #	<i>n</i> Sites	<i>n</i> Samples
<i>Clethrionomys rutilus</i> *†	northern red-backed vole	180293	15	122
<i>Dicrostonyx groenlandicus</i> *†	northern collared lemming	180328	2	14
<i>Lemmus trimucronatus</i>	brown lemming	180320	1	1
<i>Microtus longicaudus</i> *	long-tailed vole	180299	1	3
<i>Microtus miurus</i> *†	singing vole	180309	2	20
<i>Microtus oeconomus</i> *†	root vole	180298	10	51
<i>Microtus pennsylvanicus</i> *	meadow vole	180297	2	4
<i>Microtus xanthognathus</i> *	yellow-cheeked vole	180301	2	4
<i>Sorex cinereus</i>	cinereus shrew	179929	11	56
<i>Sorex hoyi</i>	pygmy shrew	179946	3	6
<i>Sorex monticolus</i>	montane/dusky shrew	179950	4	5
<i>Sorex tundrensis</i>	tundra shrew	179957	4	18
<i>Sorex ugyunak</i>	barren-ground shrew	552509	1	5
<i>Sorex yukonicus</i>	Alaskan tiny shrew	555663	1	1
<i>Synaptomys borealis</i> *	northern bog-lemming	180323	3	4
<i>Tamiasciurus hudsonicus</i>	red squirrel	180166	6	0
<i>Urocitellus paryii</i>	Arctic ground squirrel	930321	1	0

Table 2. Means and 95% confidence intervals for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, corrected $\delta^{13}\text{C}$ ($\delta^{13}\text{C}_c$) and trophic position (derived from $\delta^{15}\text{N}$), from rodent hair for 8 species of rodent at sampling locations across Alaska.

Scientific Name	<i>n</i>	Hair $\delta^{13}\text{C}$ ‰		Hair $\delta^{15}\text{N}$ ‰		Hair $\delta^{13}\text{C}_c$ ‰		Trophic Position	
		Mean	95% CL	Mean	95% CL	Mean	95% CL	Mean	95% CI
<i>C. rutilus</i>	122	-24.47	-24.59 – -24.34	4.53	4.17 – 4.89	0.31	0.29 – 0.34	2.54	2.40 – 2.69
<i>D. groenlandicus</i>	14	-25.56	-25.77 – -25.35	1.57	0.92 – 2.22	0.35	0.29 – 0.40	0.66	0.40 – 0.92
<i>M. longicaudus</i>	3	-25.21	-25.79 – -24.61	2.04	0.28 – 3.80	0.09	0.01 – 0.18	1.27	0.62 – 1.93
<i>M. miurus</i>	20	-25.47	-25.70 – -25.24	2.29	1.75 – 2.82	0.15	0.13 – 0.18	2.69	2.47 – 2.91
<i>M. oeconomus</i>	51	-25.99	-26.29 – -25.69	4.37	3.88 – 4.86	0.24	0.19 – 0.28	2.79	2.57 – 3.01
<i>M. pennsylvanicus</i>	4	-25.37	-27.05 – -23.68	5.55	4.91 – 6.19	0.20	0.03 – 0.38	2.81	1.92 – 3.70
<i>M. xanthognathus</i>	4	-25.99	-26.88 – -25.10	3.88	1.64 – 6.11	0.13	0.05 – 0.20	1.95	1.13 – 2.78
<i>S. borealis</i>	4	-28.51	-32.82 – -24.19	4.37	-0.19 – 8.94	-0.17	-0.55 – 0.22	2.24	0.90 – 3.59

Figure captions

Fig. 1. Shaded relief map of Alaska depicting 20 study-sites sampled along latitudinal and longitudinal mega-transects according to year sampled.

Fig. 2. Dual isotope plot depicting means and 95% confidence intervals for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of rodents, shrews, and five vegetation functional groups pooled across sample locations. Rodent and shrew $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ were corrected downward 2.7‰ and 2.4‰, respectively to account for trophic enrichment.

Fig. 3. Means and 95% credible intervals for dietary source proportions for four species of rodent as calculated by SIAR using five-member mixing models. Stable isotope values for rodent and vegetation samples were pooled across sites where rodent species were present.

Fig. 4. Core isotopic niche ellipses, representing fundamental niches, calculated in SIBER for eight rodent species (voles and lemmings) across Alaska. Trophic position (T_p), which was calculated from $\delta^{15}\text{N}$, is plotted against corrected $\delta^{13}\text{C}$ ($\delta^{13}\text{C}_c$) values. Standard ellipses include 1 standard deviation of the mean, or roughly 40% of data.

Fig. 5. Standard niche ellipse (solid) and convex hull (dashed) isotopic niche areas calculated in SIBER for co-occurring species at eight study sites: a) Atigun Pass, b) Chandalar River, c) Isabel Pass, d) Kenai Lowlands, e) Mountain Village, f) Nenana River, g) Sagwon Bluffs, h) White Mountains. Species include *Clethrionomys rutilus*

(northern red-backed voles; red), *Microtus miurus* (singing voles; light blue), *M. oeconomus* (root voles; dark blue), and *M. longicaudus* (long-tailed voles; pink). Trophic position (Tp), which was calculated from $\delta^{15}\text{N}$, is plotted against corrected $\delta^{13}\text{C}$ ($\delta^{13}\text{C}_c$) values.

Draft

Fig. 1. Shaded relief map of Alaska depicting 20 study-sites sampled along latitudinal and longitudinal mega-transects according to year sampled.
263x190mm (150 x 150 DPI)

Fig. 3. Means and 95% credible intervals for dietary source proportions for four species of rodent as calculated by SIAR using five-member mixing models. Stable isotope values for rodent and vegetation samples were pooled across sites where rodent species were present.

245x116mm (150 x 150 DPI)