Sources of variation in small rodent trophic niche: new insights from DNA metabarcoding and stable isotope analysis

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Intraspecific competition for food is expected to increase the trophic niche width of consumers, defined here as their diet diversity, but this process has been little studied in herbivores. Population densities of small rodents fluctuate greatly, providing a good study model to evaluate effects of competition on trophic niche. We studied resource use in five arctic small rodent populations of four species combining DNA metabarcoding of stomach contents and stable isotope analysis (SIA). Our results suggest that for small rodents the most pronounced effect of competition on trophic niche is due to increased use of secondary habitats and to habitat-specific diets, rather than an expansion of trophic niche in primary habitat. DNA metabarcoding and SIA provided complementary information about the composition and temporal variation of herbivore diets. Combing these two approaches requires caution, as the underlying processes causing observed patterns may differ between methodologies due to different spatiotemporal scales.

Keywords: herbivore; tundra food web; habitat use; trophic niche width; diet diversity; competition
1. Introduction

Intraspecific competition is often linked to an increase of a populations’ trophic niche width (1, 2). We here refer to trophic niche as a part of the multidimensional ecological niche space of a population (3, 4), defined by food resource use. Trophic niche width thus describes the size of trophic niche and can be measured as diversity of used food resources (5-7). While a link between intraspecific competition and trophic niche width may exist for many consumers, the few studies that have investigated this relationship in herbivores suggest that different mechanisms may come into play (8-11). High herbivore population density may directly induce a narrowing of the trophic niche due to reduced plant species richness under a regime of intense grazing (9, 11). In addition, competition may indirectly affect trophic niche width. Increased use of secondary habitats at higher population densities, i.e. an increase in habitat niche width (defined analogously to trophic niche width, see above) has been documented in herbivores (12, 13), although also contradictory examples exist (14). As herbivore diets often differ between habitats (15, 16), an increase in a population's habitat niche width may consequently increase its trophic niche width. However, it is clear that current understanding of processes linking competition and herbivore trophic niche width and composition is incomplete.

In arctic and sub-arctic areas, the structure and dynamics of terrestrial food webs are largely shaped by high-amplitude population cycles of herbivorous lemming and vole populations (17-20). Such density fluctuations, also found outside the Arctic (21, 22), make small rodents a very well suited model group to investigate the consequences of competition on trophic niche. Several authors have hypothesized that during peaks of population density the availability of high-quality food for small rodents is limited, leading potentially to a change in population trophic niche (23-25). On the other hand, numerous studies have assumed that small rodents do not change the taxonomic composition of their diet during population density peaks (26-28). Still, only a handful of studies have evaluated changes of
small rodent food habits during population peaks (29-31). Population density of small rodents has, however, been related to expansion of habitat use (13, 32-34). Nevertheless, the relationship between habitat use and diet remains poorly understood in most small rodent species (35). For instance, some studies have indicated that food availability is an important determinant of small rodent food selection (36, 37), whereas others have found rather small differences in small rodent diets among habitats in spite of differences in food availability (38-40). Therefore, while competition may lead to an increase in habitat niche width in small rodents, how this is reflected in the trophic niche remains little explored.

The current lack of knowledge about small rodent diets is mainly due to methodological limitations, as microhistological studies on rodent stomach or feces content are both taxonomically relatively imprecise and tedious to conduct (41). DNA metabarcoding, i.e. simultaneous identification of multiple taxa from a sample containing a mixture of DNAs by means of high-throughput sequencing of a carefully selected part of the genome (42, 43), has recently opened up possibilities to analyze herbivore stomach contents with increased taxonomic precision (41, 44-47). While DNA metabarcoding yields detailed information on the content of the latest meal, long term resource use can be assessed using stable isotopes of carbon (C) and nitrogen (N) (48, 49). Ratios of $^{13}$C/$^{12}$C and $^{14}$N/$^{15}$N (denoted as $\delta^{13}$C and $\delta^{15}$N) in a consumer's tissue reflect those of its food sources in a predictable manner (50, 51), and thus integrate information on its multidimensional trophic niche into fewer dimensions (e.g., bivariate when two isotopes are used). Consequently, isotopic ratios of a population can be described as an isotopic niche, which size can be used to assess niche width (52-54).

Combined analyses of stomach contents and stable isotopes yield higher taxonomic precision and wider timeframe, thus providing complementary insights unavailable through one method alone (55-58). To our knowledge, (58, 59) are the only ones to date who have attempted to combine stable isotope analysis and DNA-based methodology, using PCR-based taxon
identification. They found this approach to be a powerful combination, but suggest that high-throughput sequencing, as is used in DNA metabarcoding approaches, should open for further possibilities (58, 59).

Here, we combine the use of DNA metabarcoding with stable isotope analysis to investigate the relationships between population density, habitat niche and trophic niche. We also aimed to evaluate the possibilities and challenges related to the combined use of these methods for herbivore diet studies in particular. Specifically, we assessed the impacts of intraspecific competition on small rodent population trophic niche, evaluating both a) direct effects within the primary habitat and indirect effects mediated through changes in habitat use and b) trophic niche width and its composition. We always refer to the realized niche of a population (3, 4) and consider niche width as diversity of resource use, taking into account both the number of resources and relative intensity of their use (5-7). We used data from four arctic small rodent species from five populations and three distant study areas (see Table 1), across various plant communities and densities of small rodents. Assuming that an increase in population density leads to an increase in intraspecific competition, we hypothesized that it could in turn lead to H1) changes in the populations’ trophic niche width and composition and/or H2) an increased heterogeneity of habitat use, i.e. wider habitat niche. We further hypothesized that H3) the composition of the trophic niche would differ between habitats reflecting food availability and hence H4) an increase of habitat niche width would lead to a wider trophic niche.

2. Material and Methods

2.1. Study areas

The data were collected in three different Arctic study areas; Finnmark in north-eastern Norway (70° N, 27-30° E) at the border of the sub-arctic and low-arctic zones, low-arctic
Nenetsky Ridge in Nenetsky Autonomous Okrug, Russia (68° 18' N, 53° 18' E) and high-arctic Bylot Island, Nunavut, Canada (73° 9' N, 79° 59' W) (Figure 1). More than one small rodent species are found at each study area, and most of them exhibit cyclic high-amplitude population dynamics (60-62). In the Finnmark study area, the data were collected from three different study sites separated by 40 to 60 km; Ifjordfjellet (IF), Vestre Jakobselv (VJ) and Komagdalen (KO) (Figure 1), whereas at Nenetsky and Bylot Island, all samples were collected in an area within a radius of 5 km. All data collection was done during snow-free period.

In the Finnmark study area, the data were collected in three habitats; dwarf-shrub heaths (primary habitat for grey-sided vole, *Myodes rufocanus*), willow-thicket meadow mosaics (hereafter called meadows, primary habitat for tundra vole, *Microtus oeconomus*, hereafter denoted as *M. oeconomus*(Finnmark)) and shrubby wetlands. While none of these habitats can be defined as an obvious primary habitat for Norwegian lemming *Lemmus lemmus*, the species is more abundant in the heath and wetland habitats than in the meadow habitat. We chose to assign heath as the “primary habitat” for *L. lemmus* in this study, as we had a very low sample size for the wetland habitat. In Nenetsky, similar meadows, inhabited by a *M. oeconomus* population (hereafter denoted as *M. oeconomus*(Nenetsky)), were sampled. On Bylot Island, data were collected in wetland (primary habitat for brown lemming *Lemmus trimucronatus*) and mesic tundra habitats. All habitats described here refer to the summer habitat use of the respective species. Further details on vegetation within these habitat types, as well as herbivore fauna in the different study areas are described in Appendix 1, and have been published for Finnmark by (37, 63-65); for Nenetsky by (66) and for Bylot Island by (67, 68). In Table 1, we summarize the populations, years, habitats, and types of analyses for which samples were collected in each study area.
2.2. Population census data and sample collection

In Finnmark and Nenetsky, rodents were trapped as part of monitoring program using the small quadrate-method based on snap-trapping with 12 traps per quadrate over two consecutive nights (69). For each rodent species, we calculated a density index of rodents trapped per 100 trap nights per quadrate (no. rodents/24*100). We used a subset of the trapped rodents for DNA metabarcoding (n = 318 exclusively from Finnmark) and stable isotope analyses (n = 123 from Finnmark, n = 37 from Nenetsky) as described below. Further details on the trapping have been published for meadow habitat in Finnmark (64) and the spatial and temporal distribution of the sampling quadrates are described in Appendix 1.

On Bylot Island, rodents were trapped using snap-trapping and mark-recapture live-trapping (details given in Appendix 1, data published in (70)). A subset of the snap-trapped individuals was used for stable isotope samples (n = 26), in addition to individuals found dead during live-trapping (n = 36). To assess population density, we used estimates obtained through the mark-recapture trapping, which are likely to better reflect actual lemming densities than snap-trapping indices.

2.3. DNA metabarcoding data

Stomach contents of 53 L. lemmus, 111 M. oeconomus(Finnmark), and 154 M. rufocanus from Finnmark study area, collected between 2007 and 2011, were analyzed for seed plant content using DNA metabarcoding. The method is based on first amplifying seed plant DNA using the g-h primer pair which targets the P6-loop of the plastid trnL (UAA) intron and thereafter high-throughput sequencing the amplified DNA (41, 71). Laboratory analyses of the samples were done in three different batches, but we combined all raw sequencing data prior to sequence annotation to ensure that the data were comparable. The sequences were assigned to plant taxa by comparison with (i) the arctic trnL taxonomic reference library (72) (ii) a north boreal trnL taxonomic reference library constructed by sequencing 1,332 plant samples.
representing 835 species (73), and (iii) GenBank, using the program ecoTag. Further details of the bioinformatics analyses are given in Appendix 1. The resulting dataset consisted of a count of sequence reads per taxon per individual rodent. We transformed count data into proportions of plant taxa per individual stomach content to allow for inter-individual comparison. We grouped plant taxa to family level, in order to be able to include most of the data into our analyses (33% of unique sequence reads were annotated to species, 33% to genus, and 30% to family level, respectively). Even though the primer pair g-h primarily targets seed plants (Angiosperms and Gymnosperms), some ferns, horsetails and mosses were also identified. We included these into the analyses as groups “mosses” and “ferns and allies”. A substantial part of the diet of *L. lemmus* is composed of mosses, but this component of its diet consists rather uniformly of the genus *Dicranum* (74). We could therefore assume that most variation in the species diet occurs within the seed plant component and hence did not include a more comprehensive analysis of mosses in this study.

### 2.4. Stable isotope samples

Samples of small rodent muscles for carbon (δ13C) and nitrogen (δ15N) stable isotope analyses (hereafter, SIA) were collected on Bylot Island (2008 and 2010), Finnmark (2007-2008 and 2011), and Nenetsky (2007-2008). Details for SIA have been published by (75) and (76), except for minor adjustments described in Appendices 1 and 2. To estimate the variability of plant isotopic ratios between species, habitats and localities, we analyzed samples of 21 plant species (n = 280) collected in 2009 in the Finnmark study area. Details of the plant SIA are described in Appendices 1 and 2.

### 2.5. Data analysis

We used software R 2.14 for all statistical analyses (77).
2.5.1. Trophic niche based on DNA metabarcoding data

DNA metabarcoding data were available for the three populations of Finnmark (Table 1.) To evaluate the effect of population density on trophic niche width, we used as sample units groups of individuals (hereafter “density groups”) that were homogeneous in terms of species, year, season, study site (IF, VJ or KO, Figure 1), and habitat (heath, meadow or wetland). We only considered density groups with a minimum of five individuals. Due to low sample size, we grouped individuals across all habitats for *L. lemmus* (n = 51 individuals in total, 28 included in this analysis as small density groups were excluded [see above]). For each density group, we calculated an index of trophic niche width for the average diet of the group, using the Shannon entropy (equation given in (5), index denoted hereafter as TNW). We used linear regressions to test, for each species separately, whether population density index (predictor variable) had an impact on TNW (response variable). To calculate population density index for each density group, we first assigned each individual the density index from the small quadrate where it was trapped. We then calculated an average density index for each density group across individual values. We included habitat (heath or meadow) as a covariate in the models for *M. rufocanus* and *M. oeconomus* (Finnmark). We checked for model fit to assumptions using diagnostic plots.

We further examined the effect of population density and habitat on diet composition, using individuals as sampling units. We used individual diet proportions as a multivariate response variable, with population density index (i.e. density index value for an individual in the quadrate it was trapped) and habitat (i.e. the habitat where an individual was trapped) as the predictor variables of interest. We analyzed these with Principal Component Analysis with respect to Instrumental Variables (PCAIV) on centered proportions of plant families, implemented with pcaiv-function from ade4-package of the software R (78). To reduce the effect of rare observations, we removed individuals that had fed only on one plant family (n = 3, 1, and 2 for *M. rufocanus*, *M. oeconomus* (Finnmark) and *L. lemmus*, respectively), as well as
plant families observed in only one individual \( n = 3, 2, \) and 6 for \( M. \) rufocanus, \( M. \) oeconomus(Finnmark) and \( L. \) lemmus, respectively). We used forward selection with permutation (5,000 replicates) implemented with forward.sel- function of the packfor-package (79), to test whether covariates should be included (site (IF, VJ or KO), season (summer or autumn), and year (2007-2011)). We only retained covariates significant at \( \alpha = 0.05 \) level, but always kept habitat and density in the analysis.

To evaluate the effect of habitat use expansion on trophic niche width, we used as sample units groups of individuals which were homogenous in terms of species, year, season and study site. For each group, we calculated TNW in two ways; \( TNW_{(all \, habitats)} \) including all individuals and \( TNW_{(primary \, habitat)} \) including only individuals from primary habitat. We then assessed whether \( TNW_{(all \, habitats)} \) was significantly larger than \( TNW_{(primary \, habitat)} \), using a re-sampling approach. For each group, we drew 100 times a random combination of individuals (with \( n \) equaling that of individuals from primary habitat in the respective group), and calculated TNW for these. However, when the number of possible different combinations was smaller than 100, we calculated TNW for all possible combinations. This was the case for the following groups: \( M. \) rufocanus 2007 summer KO and VJ, 2010 autumn KO; \( M. \) oeconomus 2007 summer KO and 2011 summer KO; \( L. \) lemmus 2010 autumn IF and 2011 autumn IF. When the observed difference \( TNW_{(all \, habitats)} - TNW_{(primary \, habitat)} \) was above the upper 95% confidence interval of the re-sampled difference (i.e. \( TNW_{(all \, habitats)} - TNW_{(resampled)} \)), we considered that \( TNW_{(all \, habitats)} \) was significantly larger than \( TNW_{(primary \, habitat)} \).

2.5.2. Isotopic niche

Analyses of isotopic niche covered all five study populations (Table 1). We used the variability of isotopic ratios – a measure of isotopic niche - as a proxy for tracking the changes in the trophic niche (52, 53). For all analyses of rodents’ isotopic niche, we measured isotopic niche width (hereafter referred as INW) as the spread of stable isotope ratios in \( \delta- \)
space (i.e. a two-dimensional space with one axis for $\delta^{13}$C and one axis for $\delta^{15}$N; see Figure 2 and 3), estimated via the mean distance to centroid (80, 81). We evaluated changes in isotopic niche composition based on differences in centroid locations (81). For each measure, we used groups of individuals as sampling units and tested for the significance of differences between their distance to centroid and centroid locations using permutation tests described by (81), with 10,000 replicates. See supplementary Table S1 for numbers of individuals included in the different analyses.

To evaluate the effect of population density on isotopic niche width, we divided all five rodent populations into groups of “low” and “high” density. We thus used population density as a categorical variable, to be able to compare groups of individuals, as required by methods of assessing isotopic niche width (80, 81). For Finnmark and Nenetsky, we first assigned to each individual a population density index value (i.e. the density index value from the small quadrate where it was trapped). We then assigned individuals with density index values <10 or >=10 to the “low” and “high” groups, respectively. The “low” index value thus corresponds to one or two individuals trapped in a grid during a trapping event (2/24*100 = 8.3), “high” corresponding to three or more individuals (3/24*100 = 12.5). In Table 1, we summarize the years, seasons, sites, and habitats from which individuals of different populations were included in this analysis. On Bylot Island, population densities in wetland habitats (primary habitat for *L. trimucronatus*) differed little between 2008 and 2010 (Figure 4). However, during 2008 population densities were decreasing, and little spillover of *L. trimucronatus* from wetland to mesic habitat occurred (Figure 4). In 2010 population densities were increasing, and *L. trimucronatus* was abundant in mesic habitat, indicating saturation of wetland habitats. We therefore assigned individuals trapped in 2008 into density group “low” and individuals trapped in 2010 into group “high”. Within all populations, we assessed difference in INW between “low” and “high” groups by testing for difference in mean
distance to centroid as described above. Furthermore, to evaluate whether a populations’ isotopic niche composition was affected by population density, we tested whether centroid locations of “high” and “low” groups differed (see conceptual illustration of these analyses in Figure 2). We analyzed the differences between low and high densities in two ways; using all individuals and individuals trapped from primary habitats only. For *M. oeconomus* (Nenetsky) all individuals were collected from primary habitat and we therefore did only one analysis.

To evaluate the effect of habitat use expansion on isotopic niche width, we calculated populations INW in two ways; including only individuals from the primary habitat, $INW_{(primary\ habitat)}$, and including all individuals irrespective of habitat, $INW_{(all\ habitats)}$. We then tested whether $INW_{(all\ habitats)}$ was significantly larger than $INW_{(primary\ habitat)}$. To assess whether habitat had an impact on isotopic niche composition, we compared pairs of habitat-specific groups of individuals in terms of centroid locations. We included in each pairwise comparison a species primary habitat and one of the secondary habitats. When we had data from several secondary habitats, we compared each of these separately against the primary habitat.

We evaluated the role of confounding effects (site, season, and year) for the observed patterns visually, using isotopic bi-plots. Because we found no directional differences between sites or years in Finnmark (see Supplementary Figure S1 in Appendix 2), we included all data in the analyses. However, as we did find some seasonal patterns, we present them together with the results for density and habitat (Figure 3), and take them into account in our interpretation of results.

2.5.3. Population density data and spillover to adjacent habitats

We assessed the effect of population density on habitat for the three populations of the Finnmark study area (Table 1). In these analyses, we included a subset of the sampling quadrates which are situated so that the study design in each study site was balanced including an equal number of heath and meadow quadrates (until 2008, numbers of quadrates per
habitat were 12 in KO, 13 in VJ and 12 in IF, while from 2009 on they were 10[KO], 9[VJ] and 9[IF]). These quadrates were spatially arranged as pairs, each pair including a quadrat from each habitat. In these analyses, we used pairs of quadrates as sampling units and analyzed for each species separately whether an increase of the number of individuals trapped in primary habitat (predictor variable) was related to an increase of the number of individuals trapped in secondary habitat (response variable). We run Poisson regressions, implemented with lmer-function of the R-package lme4 (82), including year (2007 to 2011), season (summer or autumn), site (KO, VJ and IF) and quadrat pair identity (37 levels) in the models as random variables. We checked model fit to assumptions using diagnostic plots.

3. Results

3.1. Density and trophic niche width (TNW and INW)

We found little indication that trophic niche width of small rodents increased with population density. TNW (analysed for the three Finnmark populations, Table 1) had no significant correlation with population density index in any of the tested populations, although M. oeconomus (Finnmark) had a weak increasing trend in its primary habitat (Figure 5, Table 2). INW (analysed for all populations, Table 1), based on mean distance of individuals to centroid, increased significantly with population density only for L. lemmus, when individuals from either all habitats or the primary habitat only were included (Figure 3). When we included only individuals from primary habitat, L. trimucronatus also showed an increase of INW with density. However, we also found an opposite effect of density on INW in M. oeconomus (Finnmark) when individuals from all habitats were included, but not when individuals from only primary habitat were included (Figure 3, Appendix 2; Supplementary Table S2).
3.2. Density and trophic niche composition

Based on DNA metabarcoding data, density had no significant effect on trophic niche composition of any of the studied species (populations included in the analyses are in Table 1, results in Figure 6, Appendix 2; Supplementary Tables S3 and S4). Using stable isotope data, we found species-specific patterns of the effects of density on isotopic niche composition (populations included in the analyses are in Table 1, results in Figure 3, Appendix 2; Supplementary Table S2). Centroid locations differed between low-density and high-density groups for all populations but *L. lemmus* (Figure 3, Appendix 2; Supplementary Table S2).

However, for *M. oeconomus* (Finnmark) the pattern disappeared when only individuals from primary habitat were considered. In addition, the density-related patterns could not be confidently distinguished from those caused by season in *M. rufocanus* and *L. trimucronatus* (Figure 3). Data for these populations tended to be collected during different seasons in high and low population densities, and the variation of the individual stable isotope ratios due to density was correlated with the season (Figure 3).

3.3. Density and habitat use expansion

Number of individuals trapped in secondary habitat increased with number of individuals trapped in primary habitat for all three species tested (i.e. all species from Finnmark, Table 1), (Table 3), indicating density-driven spillover from primary to secondary habitats.

3.4. Habitat and trophic niche composition

Based on DNA metabarcoding data, habitat had an impact on trophic niche composition (populations included in the analyses are in Table 1, results in Figure 6, Appendix 2; see also Supplementary Tables S3 and S4). Predictor variables along the first PCAIV-axis predicted 20%, 26%, and 22% of the variation in our data for *M. rufocanus*, *M. oeconomus* (Finnmark), and *L. lemmus*, respectively (Figure 6, Appendix 2; Supplementary Tables S3 and S4). Variables
found significant by forward selection were habitat and site (IF differed from VJ but not from KO) for *M. rufocanus*, habitat and year for *M. oeconomus*(Finnmark), and site (IF differed from KO but not from VJ) for *L. lemmus* (Appendix 2; Supplementary Table S4). Habitat was still the most influential predictor explaining the first PCAIV axis for all three species (Figure 6, Appendix 2; Supplementary Table S4), suggesting that for *L. lemmus* the effect of habitat was not detected in forward selection due to low sample size (n = 35, 11 and 5 for heath, meadow and wetland habitats, respectively). Diets reflected the abundance relationships of plant families within the different habitats (described in detail in (37)). For both vole species, ericoid shrubs were associated with heath habitat, whereas forb families, especially Polygonaceae and Ranunculaceae, were associated with meadow habitat. For lemmings, grasses (Poaceae) were associated with heath habitat whereas sedges (Cyperaceae) were associated with wetland and meadow habitats.

Based on stable isotope data, i.e. differences of centroid locations, habitat had an impact on isotopic niche for *M. rufocanus* and *M. oeconomus*(Finnmark). This was indicated by the significant difference of centroid location between wetland habitat and primary habitat of the respective species (Figure 3, Appendix 2; Supplementary Table S2). Differences between heath and meadow observed using DNA metabarcoding were not found in the stable isotope data, indicating that the difference in diets between heath and meadow habitats was smaller than between these habitats and the wetland habitat (populations included in analyses are given in Table 1).

### 3.5. Habitat use expansion and trophic niche width

Patterns in the effect of habitat use expansion on trophic niche width differed among methods. Based on DNA metabarcoding data, TNW\(_{\text{all habitats}}\) was higher than TNW\(_{\text{primary habitat}}\) in all but two of the 17 groups tested (Table 4). For all of these groups, the observed difference was larger than the difference between TNW\(_{\text{all habitats}}\) and TNW\(_{\text{resampled}}\) (Table 4), indicating a
significant increase of TNW with habitat use heterogeneity. On the contrary, stable isotope
data showed no similar trends, as we found no difference between INW_{all habitats} and
INW_{primary habitat} based on mean distance to centroid (populations included in analyses are
given in Table 1, results in Figure 3, Appendix 2; Supplementary Table S2).

4. Discussion

4.1. Population density and small rodent trophic niche

We found that habitat use was an important determinant of trophic niche at short time scales,
based on the DNA metabarcoding data. Habitat was an important determinant of an
individual's diet (supporting H3), and heterogeneity in habitat use consequently increased
populations’ trophic niche width (supporting H4). Furthermore, we observed density-driven
spillover from primary to secondary habitats (supporting H2) for all three species in the
Finnmark study area. Spillover to adjacent habitats has frequently been related to high
population densities in small rodents (13, 32-34). Several driving forces have been suggested
for such density-driven increase of population habitat niche width, most prominently resource
competition and social competition (35, 83-86). While we cannot determine the cause of the
spillover in our study system, we argue that it is unlikely to be caused by competition for
food. In the primary habitat, we found no indication for an effect of density on trophic niche
width in most populations, except for the two lemming populations over long time scales, as
indicated by stable isotope data (H1 being supported only for these populations). Thus,
population density did not have a strong impact on diet diversity in the studied small rodent
populations. High population density of small rodents seems hence to induce an increase of
habitat niche width before competition for food reaches levels that impact population trophic
niche width.
Our results imply that habitat-specific food availability is one of the most important
determinants of small rodent trophic niche composition. For example, *M. oeconomus* (Finnmark)
in the meadow habitats of Finnmark study area select for forbs and willows (37). Availability
of these plant groups is lower in the heaths than in the meadows, and their taxonomic
composition differs (37). Subsequently, *M. oeconomus* (Finnmark) need to adjust their feeding
habits in different habitats, which is illustrated by our results. The effect of habitat niche
expansion on trophic niche width is, however, likely to differ between small rodent
populations based on the similarity of plant species pools between habitats. For example, the
most important vascular plant food item of *L. lemmus* in the Finnmark study area is the grass
*Avenella flexuosa* (74). This grass species is abundant in both heath and meadow habitats
(87), and thus *L. lemmus* probably faces comparatively little need to adjust its diet when
moving between these habitats. This illustrates that some herbivore species may maintain
their preferred diet in another habitat simply because the preferred food items are available
there as well. Furthermore, food availability can be strongly reduced by predation risk, which
again is modified by the availability of sheltering vegetation (88). Hence, the extent to which
a populations’ habitat use modifies its trophic niche width most likely varies between species
based on both their food preferences as well as habitat-specific availability of food and shelter
from predators.

It has been suggested that certain plant species would be included in small rodent diets
exclusively at high population densities, causing such a reduction of diet quality that the
population dynamics are affected (23-25). Our results indicate that this is unlikely to be the
case, at least for the population densities observed in this study. We found species-specific
patterns in the direct effects of density on population trophic niche width within the primary
habitat, and little unambiguous evidence for a change in population trophic niche composition
due to density. On the other hand, food availability is an important determinant of small
rodent diets, both among habitats, as indicated by our results, and within habitats (37). Any change in an individual’s diet, which is caused by population density, is therefore likely to depend on what is available for different individuals in terms of food quality and quantity. These, in turn, can be modified by various local factors, such as predation risk and shelter availability. Individuals can, therefore, be expected to differ in terms of how population density impacts their diet. It thus seems unlikely that the quality of a single food item, included in the diet of a rodent population only at high population densities, would have such impacts on reproduction or mortality that the population dynamics would be affected.

Our results differ between species in many aspects, indicating that different herbivore species, even within a relatively homogeneous guild, may show different trophic responses to increased density. One explanation of such differences is that the impact of competition on herbivore diet is likely influenced by the degree of specialization of the herbivores. For example, lemmings have in general more specialized feeding habits than voles (16, 37, 74). Consequently, they may experience exploitation competition, causing a diversification of diet, at population densities which would not impact the trophic niche width of voles. Herbivore species trophic niche width response to high densities may also be partly determined by the impact of herbivores on vegetation. For example, the results of (9, 11) suggest that intensive grazing by ungulates would reduce plant species richness, thus leading to a decreased trophic niche width. High population densities of ungulates may persist over long time periods and indeed often have drastic effects on vegetation diversity (89-91). On the other hand, the period of intense grazing by cyclic small rodent populations lasts only a year or two, and impact on vegetation is sometimes limited (e.g. Bylot Island; (92)). Small rodents may thus interact with vegetation diversity in a different manner than larger herbivores. Our results underline that the effects of competition on the trophic niche of herbivore population can be both direct and indirect, and depend greatly on the ecology of the species in question. For
instance the degree of diet specialization, interplay between high population densities and
vegetation diversity as well as dispersal to adjacent habitats may modify either the direct or
indirect effects of competition. This urges further studies on the effects of competition on
herbivore trophic niches to consider, in addition to direct effects, both indirect effects and
interactions between herbivores and their food plants.

4.2. Usage of stable isotopes and DNA metabarcoding in herbivore diet studies

The use of DNA metabarcoding and SIA in diet studies has recently been discussed in detail
in publications focusing on one of the methods (47, 49, 93). We focus here on the
combination of these two methods, illustrating how they may be used in a complementary
manner in diet studies.

We obtained several method-specific results. For example, we found clear differences
in trophic niche composition between heath and meadow habitats for the vole species using
DNA metabarcoding. SIA, on the other hand, indicated that diets of voles differed between
their respective primary habitat and wetland habitat, but not between heath and meadow
habitats. These discrepancies illustrate the importance of different temporal resolution
between these two types of data. While DNA metabarcoding of stomach contents captures the
last meal, stable isotopes can incorporate information over a much longer time-scale (94, 95).
Although no data on muscle turnover rates of our study species exist, based on data from
other rodent species (95, 96) we can assume that the present isotopic ratios reflect average
diets during the last month. Because plant species identity was the main source of plant
isotopic variation and habitat was a strong predictor of short-term diets, we would have
expected habitat-specific differences in small rodent stable isotope ratios. As this was not the
case, the sampled small rodents were probably not exclusively feeding in the habitat where
they were captured during the last month. Some of the sampled individuals may for example
have migrated from primary to secondary habitats or included several habitats in their home-
ranges. While the sampling quadrates covering heath and meadow habitats were situated in each other’s vicinity, the wetland habitat quadrates were spatially more segregated. Thus, food availability in the area where an individual was moving the month prior to trapping differed probably less between heath and meadow than between wetland and the other habitats. This underlines the importance of considering processes at appropriate temporal and spatial scales, such as the effect of habitat-specific food availability over the short-term and residency time within habitat over the longer term.

In our study, DNA metabarcoding could describe the composition of current diets and their spatial variability. However, the difference in food availability between habitats is probably greater at plant species level than at the family level. Hence, the actual effect of habitat-specific food availability on diets is probably larger than what we observed in our family level analyses. Future studies may therefore benefit from new developments of DNA metabarcoding offering higher species level resolution (43). On the other hand, stable isotope data illustrated that spatial variability of trophic niche does not necessarily persist over time. In principle, stable isotope ratios of different tissues alone could give indication of the spatial and temporal variation in diets (6, 54). However, herbivore diet composition cannot, in most cases, be inferred from their stable isotope ratios due to the large number of potential food items and the overlap between their stable isotope ratios (e.g. present study). However, a combination of SIA and DNA metabarcoding may elucidate herbivore feeding ecology when both current diet composition and temporal variability are of interest. For example, when parts of the life-cycle of the herbivore in question are cryptic or otherwise inaccessible, stable isotope samples from a tissue with slow turnover can provide a way to study past diets. For small rodents, such an application could be especially of interest in studying feeding habits during winter, which is a critical season in terms of food limitation, but difficult to study otherwise. However, a comprehensive understanding of the temporal variation in underlying
plant stable isotope ratios would be required to properly exploit the possibilities of stable isotopes in describing temporal changes of herbivore diets.

The approach outlined above to combine DNA metabarcoding and SIA is discussed with a focus on diet studies of terrestrial herbivores, while different approaches may come into question for different types of consumers. For example, DNA metabarcoding of predator diets is often more difficult than that of herbivores, due to the inherent problem of prey DNA getting swamped by the predators DNA (47). For SIA the situation is the opposite, i.e. predator diet composition is often easier to assess than that of herbivores, due to a lower number of food items with more distinct stable isotope ratios (97). On the other hand, depending on the question very different analytic approaches could be used, as is illustrated by (58), who evaluated different carbon sources of a river ecosystem rather than attempting to quantify consumer food sources. Hence, the suitability of a combination of DNA metabarcoding and SIA should be carefully assessed based on the specific study systems and questions.

Conclusions

Our results indicate that for arctic small rodents, the impact of high population density is mostly manifested as spillover to adjacent habitats before the competition for food in primary habitat is strong enough to have an impact on population trophic niche width or composition. Small rodent diets reflect food availability, and hence a density-driven increase in population habitat niche width leads to an increase in population trophic niche width as well. However, the effects of competition on herbivore trophic niche can differ between species or guilds of herbivores, while the roles of different potential drivers, such as temporal persistence of intensive grazing and degree of diet specialization remain unknown. To evaluate these drivers, a combination of DNA metabarcoding and SIA can be a useful approach, especially when both current diet composition and temporal changes are in the focus. However, this
methodological approach should be used with caution and the potential pitfalls assessed thoroughly.

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Conflict of interest

L.G. is one of the co-inventors of a patent concerning g-h primers and the subsequent use of the P6 loop of the chloroplast trnL (UAA) intron for plant identification using degraded template DNA. These patents only restrict commercial applications and have no impact on the use of this locus by academic researchers.

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Table 1. Summary of populations, sample types, analyses and sample sizes included in this study.

<table>
<thead>
<tr>
<th>Population</th>
<th>DNA</th>
<th>SIA</th>
<th>H</th>
<th>Analyses</th>
<th>Comparisons</th>
<th>n group</th>
<th>n ind</th>
<th>Data included</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lemmus lemmus, Finnmark, Norway</td>
<td>Yes</td>
<td>Yes</td>
<td>1</td>
<td>DNaNiche width ~ density</td>
<td>Individuals from same year/season/site</td>
<td>4</td>
<td>28</td>
<td>2007, 2010, 2011; H, M, W; September; VJ, KO</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>4</td>
<td>DNaNiche width ~ habitat use</td>
<td>Individuals from same year/season/site/habitat</td>
<td>2</td>
<td>34</td>
<td>2007, H, M, W; September; VJ, KO</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>1,3</td>
<td>DNaNiche composition</td>
<td>-</td>
<td></td>
<td>51</td>
<td>2007-2011, H, M; July, September, IF, VJ, KO</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>1,3,4</td>
<td>All SIANiche analyses</td>
<td>Density class groups / habitat groups</td>
<td>2/3</td>
<td>28 (16)</td>
<td>2007; H, M, W, September; VJ, KO</td>
</tr>
<tr>
<td>Microtus oeconomus, Finnmark, Norway</td>
<td>Yes</td>
<td>Yes</td>
<td>1</td>
<td>DNaNiche width ~ density</td>
<td>Individuals from same year/season/site/habitat</td>
<td>7</td>
<td>94</td>
<td>2007, 2011; H, M; July, September; VJ, KO</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>4</td>
<td>DNaNiche width ~ habitat use</td>
<td>Individuals from same year/season/site/habitat</td>
<td>3</td>
<td>61</td>
<td>2007, 2011; H, M; July, September; VJ, KO</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>1,3</td>
<td>DNaNiche composition</td>
<td>-</td>
<td></td>
<td>111</td>
<td>2007-2011, H, M; July, September; IF, VJ, KO</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>1,3,4</td>
<td>All SIANiche analyses</td>
<td>Density class groups / habitat groups</td>
<td>2/3</td>
<td>36 (18)</td>
<td>2007-2011, H, M, W; June, July, September; IF, VJ, KO</td>
</tr>
<tr>
<td>Myodes rufocanus, Finnmark, Norway</td>
<td>Yes</td>
<td>Yes</td>
<td>1</td>
<td>DNaNiche width ~ density</td>
<td>Individuals from same year/season/site/habitat</td>
<td>11</td>
<td>128</td>
<td>2007-2011, H, M; July, September; IF, VJ, KO</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>4</td>
<td>DNaNiche width ~ habitat use</td>
<td>Individuals from same year/season/site/habitat</td>
<td>8</td>
<td>110</td>
<td>2007-2011, H, M; July, September; IF, VJ, KO</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>1,3</td>
<td>DNaNiche composition</td>
<td>-</td>
<td></td>
<td>153</td>
<td>2007-2011, H, M; July, September; IF, VJ, KO</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>1,3,4</td>
<td>All SIANiche analyses</td>
<td>Density class groups / habitat groups</td>
<td>2/3</td>
<td>59 (31)</td>
<td>2007-2011, H, M; June, July, September; IF, VJ, KO</td>
</tr>
<tr>
<td>Lemmus trimucronatus, Bylot Island, Canada</td>
<td>No</td>
<td>Yes</td>
<td>1,2</td>
<td>SIANiche all analyses</td>
<td>Years / habitat groups</td>
<td>2/2</td>
<td>62 (36)</td>
<td>2008, 2010; mesic, wet; June, July, August</td>
</tr>
<tr>
<td>Microtus oeconomus, Nenetsky, Russia</td>
<td>No</td>
<td>Yes</td>
<td>1</td>
<td>SIANiche ~ density</td>
<td>Density class groups</td>
<td>2</td>
<td>37 (37)</td>
<td>2007, 2008; meadow; July, August</td>
</tr>
</tbody>
</table>

Subscript Table 1: Column “DNA”= DNA metabarcoding data; column “SIA”= stable isotope analyses; column “H”= number of hypotheses presented in the introduction (H1-H4); column “Analyses” = analyses (“DNaNiche” = analyses using DNA-data, “SIAniche” = analyses using stable isotope data); column “n group” = number of sampling unit groups (for isotopic niche, first number is for density class groups, second number for habitat groups); column “n ind” = number of individuals (for isotopic niche, first number is all individuals, second number individuals from primary habitats); column “Data included” = samples included (years; habitats (for Finnmark, H=heath, M=meadow and W=wetland); months; sites (for Finnmark, IF= Ifjord, VJ=Vestre Jakobselv, KO= Komagdalen).
Table 2. Effect of population density index on the total niche width (stomach content data, Finnmark study area, Norway). Parameter estimates based on linear regression. Intercept level for habitat is heath. Predictor variables for which 90% or 85% confidence interval does not cross zero are denoted in bold or italics, respectively.

<table>
<thead>
<tr>
<th>Species</th>
<th>Predictor</th>
<th>Est.</th>
<th>95% CI</th>
<th>$R^2_{\text{adjusted}}$</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Myodes rufocanus</em></td>
<td>Intercept</td>
<td>1.35</td>
<td>0.76, 1.94</td>
<td></td>
</tr>
<tr>
<td>(n = 11 groups)</td>
<td>Density</td>
<td>0.02</td>
<td>-0.03, 0.06</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Habitat (M)</td>
<td>0.26</td>
<td>-0.18, 0.69</td>
<td>-0.0007</td>
</tr>
<tr>
<td><em>Microtus oeconomus</em></td>
<td>Intercept</td>
<td>1.63</td>
<td>1.00, 2.28</td>
<td></td>
</tr>
<tr>
<td>(n = 7 groups)</td>
<td>Density</td>
<td>0.02</td>
<td>-0.01, 0.05</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Habitat (M)</td>
<td>-0.47</td>
<td>-1.04, 0.05</td>
<td>0.51</td>
</tr>
<tr>
<td><em>Lemmus lemmus</em></td>
<td>Intercept</td>
<td>1.56</td>
<td>-1.33, 3.26</td>
<td></td>
</tr>
<tr>
<td>(n = 4 groups)</td>
<td>Density</td>
<td>-0.006</td>
<td>-0.12, 0.10</td>
<td>-0.45</td>
</tr>
</tbody>
</table>
Table 3. The effect of population density index in primary habitat on population density index in secondary habitat (Finnmark study area, Norway). Parameter estimates from generalized linear mixed effect model with Poisson-distribution. For all populations, n = 316 trapping quadrate pairs. Response variable (i.e. density in secondary habitat) is given below species name. Estimates for intercept and fixed predictor variable (i.e. density in primary habitat, M denotes meadow and H heath) are shown with standard error, z-value and p-value of the Wald z-test, and for random effects with standard deviation of variance (SD, random effects). Predictor variables which had a significant effect (defined as p < 0.05) are denoted in bold.

<table>
<thead>
<tr>
<th>Species</th>
<th>Estimate (SE)</th>
<th>Z</th>
<th>p</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Intercept</td>
<td>Z</td>
<td>p</td>
<td>SD</td>
</tr>
<tr>
<td>M. rufocanus</td>
<td>-2.86 (0.93)</td>
<td>-3.07</td>
<td>0.002</td>
<td></td>
</tr>
<tr>
<td>Meadow</td>
<td>Density (H)</td>
<td>0.13 (0.06)</td>
<td>2.03</td>
<td>0.04</td>
</tr>
<tr>
<td></td>
<td>Quadrature pair</td>
<td>0.92</td>
<td>0.02</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Site</td>
<td>1.14</td>
<td>0.005</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Year</td>
<td>1.23</td>
<td>0.0005</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Season</td>
<td>0.30</td>
<td>0.0005</td>
<td></td>
</tr>
<tr>
<td>M. oeconomus</td>
<td>-4.27 (1.21)</td>
<td>-3.53</td>
<td>0.0004</td>
<td></td>
</tr>
<tr>
<td>Heath</td>
<td>Density (M)</td>
<td>0.19 (0.05)</td>
<td>3.56</td>
<td>0.0004</td>
</tr>
<tr>
<td></td>
<td>Quadrature pair</td>
<td>0.87</td>
<td>0.0005</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Site</td>
<td>0.89</td>
<td>0.0005</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Year</td>
<td>1.98</td>
<td>0.0005</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Season</td>
<td>0.60</td>
<td>0.0005</td>
<td></td>
</tr>
<tr>
<td>L. lemmus</td>
<td>-3.78 (1.46)</td>
<td>-2.59</td>
<td>0.01</td>
<td></td>
</tr>
<tr>
<td>Meadow</td>
<td>Density (H)</td>
<td>0.12 (0.05)</td>
<td>2.67</td>
<td>0.008</td>
</tr>
<tr>
<td></td>
<td>Quadrature pair</td>
<td>0.60</td>
<td>0.0005</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Site</td>
<td>0.87</td>
<td>0.0005</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Year</td>
<td>2.67</td>
<td>0.0005</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Season</td>
<td>0.64</td>
<td>0.0005</td>
<td></td>
</tr>
</tbody>
</table>
Table 4. Difference of total niche width (TNW) between groups of small rodent individuals from all habitats and primary habitat only, Finnmark study area, Norway. Column “Diff. obs.” refers to the observed difference (i.e. $TNW_{(all\ habitats)} - TNW_{(primary\ habitat)}$). Column “Diff. resampled” refers to mean (95% CI) difference between $TNW_{(all\ habitats)}$ and $TNW_{(resampled)}$. Groups for which the observed difference was higher than the upper 95% CI limit of the resampled difference are written in bold.

<table>
<thead>
<tr>
<th>Species</th>
<th>Year</th>
<th>Season</th>
<th>Site</th>
<th>Diff. obs.</th>
<th>Diff. resampled</th>
<th>N</th>
<th>Prop</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Myodes rufocanus</em></td>
<td>2007</td>
<td>autumn</td>
<td>KO</td>
<td>0.12</td>
<td>0.005 (-0.002, 0.01)</td>
<td>26</td>
<td>0.92</td>
</tr>
<tr>
<td></td>
<td>2007</td>
<td>summer</td>
<td>KO</td>
<td>0.01</td>
<td>0.004 (-0.0006, 0.01)</td>
<td>23</td>
<td>0.96</td>
</tr>
<tr>
<td></td>
<td>2007</td>
<td>autumn</td>
<td>VJ</td>
<td>0.19</td>
<td>0.02 (0.007, 0.03)</td>
<td>30</td>
<td>0.87</td>
</tr>
<tr>
<td></td>
<td>2008</td>
<td>autumn</td>
<td>IF</td>
<td>0.47</td>
<td>0.13 (0.10, 0.17)</td>
<td>13</td>
<td>0.46</td>
</tr>
<tr>
<td></td>
<td>2008</td>
<td>summer</td>
<td>IF</td>
<td>0.18</td>
<td>0.10 (0.08, 0.12)</td>
<td>12</td>
<td>0.58</td>
</tr>
<tr>
<td></td>
<td>2010</td>
<td>autumn</td>
<td>IF</td>
<td>-0.014</td>
<td>0.05 (0.03, 0.07)</td>
<td>13</td>
<td>0.69</td>
</tr>
<tr>
<td></td>
<td>2010</td>
<td>autumn</td>
<td>KO</td>
<td>0.43</td>
<td>0.32 (0.28, 0.37)</td>
<td>5</td>
<td>0.60</td>
</tr>
<tr>
<td></td>
<td>2011</td>
<td>summer</td>
<td>IF</td>
<td>0.43</td>
<td>0.18 (0.16, 0.21)</td>
<td>12</td>
<td>0.50</td>
</tr>
<tr>
<td><em>Microtus oeconomus</em></td>
<td>2007</td>
<td>autumn</td>
<td>KO</td>
<td>0.19</td>
<td>0.03 (0.02, 0.05)</td>
<td>25</td>
<td>0.80</td>
</tr>
<tr>
<td>(Finnamrk)</td>
<td>2007</td>
<td>summer</td>
<td>KO</td>
<td>0.07</td>
<td>0.002 (-0.001, 0.01)</td>
<td>31</td>
<td>0.97</td>
</tr>
<tr>
<td></td>
<td>2011</td>
<td>autumn</td>
<td>KO</td>
<td>0.5</td>
<td>0.31 (0.22, 0.35)</td>
<td>8</td>
<td>0.50</td>
</tr>
<tr>
<td></td>
<td>2011</td>
<td>autumn</td>
<td>VJ</td>
<td>0.24</td>
<td>0.09 (0.08, 0.11)</td>
<td>22</td>
<td>0.50</td>
</tr>
<tr>
<td><em>Lemmus lemmus</em></td>
<td>2007</td>
<td>autumn</td>
<td>KO</td>
<td>0.18</td>
<td>0.04 (0.03, 0.06)</td>
<td>20</td>
<td>0.75</td>
</tr>
<tr>
<td></td>
<td>2007</td>
<td>autumn</td>
<td>VJ</td>
<td>0.37</td>
<td>0.04 (0.02, 0.07)</td>
<td>19</td>
<td>0.68</td>
</tr>
<tr>
<td></td>
<td>2010</td>
<td>autumn</td>
<td>IF</td>
<td>0.44</td>
<td>0.15 (-0.01, 0.41)</td>
<td>5</td>
<td>0.60</td>
</tr>
<tr>
<td></td>
<td>2011</td>
<td>autumn</td>
<td>IF</td>
<td>0.63</td>
<td>0.16 (-0.01, 0.45)</td>
<td>5</td>
<td>0.60</td>
</tr>
</tbody>
</table>

Subscript Table 4: Column “N” = number of individuals for $TNW_{(all\ habitats)}$; column “prop” = proportion of N consisting of individuals for primary habitat.
Figure captions

Figure 1. Map of the study areas. Small map presents the study sites within Finnmark study area, Norway (IF = Ifjordfjellet, VJ = Vestre Jakobselv, KO = Komagdalen). Color codes (A to E) represent vegetation zones of the Arctic, according to (98): A-Polar desert; B-High-Arctic tundra; C-Typical Arctic tundra; D-Low Arctic tundra; E: Arctic Shrub-tundra.

Figure 2. Conceptual representation of isotopic niche width (INW) and composition, as used in the present study.

Figure 3. Stable isotope ratios of carbon and nitrogen for individuals from five populations of small rodents, data from all the three study areas. Populations are shown on different rows. Columns show analyses within populations; “density all” = population density groups; “density primary” = population density groups including individuals from primary habitats only; “habitat” and “season”. For the test of 1) difference in isotopic niche composition between groups we show centroid coordinates of each group (larger points) and p-values for significant differences between these (below the legend). For the test of 2) isotopic niche width we give 90% confidence ellipses, bars in lower right corner showing mean (with SE) distance to centroid (at the scale of the y-axis of the respective plot) and p-values for significantly higher distances to centroid above the bar in question. In the habitat analyses the category “combined” shows all habitats. We tested whether isotopic niche width of combined habitats differed from that of primary habitat. Letters indicate which groups were compared (H = heath, M = meadow, W = wetland). More details are given in Appendix 2; Supplementary Table S2. Empty plots indicate lack of data.

Figure 4. Population dynamics of small rodents in the study areas during years of sampling. For Finnmark population density index (individuals / 100 trap-nights) is estimated as the mean across heath and meadow quadrates. For Nenetsky only data from meadow-habitat are included. For Finnmark and Nenetsky J=July, A=August, S=September, for Bylot Island Jn=June, Jl=July (Jl1 early July, Jl2 late July), A=August. Data from Finnmark is separated between study sites ; KO= Komagdalen, VJ = Vestre Jakobselv, IF = Ifjordfjellet.

Figure 5. Total niche width (TNW) and population density index (individuals / 100 trap nights) for the three small rodent populations in the Finnmark study area.
**Figure 6.** Population density (den) and habitat (hab) effects on trophic niche composition (i.e. stomach content proportions based on DNA metabarcoding data) for the three small rodent populations in the Finnmark study area. Upper panels show unconstrained PCA plots, middle panels PCA constrained with predictor variables which are shown in lower panels (PCAIV & PCAIV loadings). The degree of similarity between PCA and PCAIV plots reflects the extent to which predictor variables can account for the structure in diet variation. If a plant family (in PCAIV plot) is in the vicinity of a predictor variable vector (PCAIV loading plot), they are positively correlated. X-axes represent 1st PCA /PCAIV axis, y-axes 2nd PCA/PCAIV axis. Inset plots show eigenvalues for each analysis, 1st bar to the left representing 1st PCA/PCAIV axis (lengths of 1st axes given in subscript below the figure). Plant family names have been abbreviated to three first letters (see subscript below the figure; open font is used to clarify overlapping names), as is done for predictor variables (PCAIV loadings plots; habM = meadow, habW = wetland, siteKO = Komagdalen, siteVJ = Vestre Jakobselv). The grey box in the middle represents all remaining plant families. PCAIV results are given in Supplementary Tables S3 and S4. For example, variability in *M. oeconomus* diet was for a large part accounted by variability in proportion of Polygonaceae (uppermost panel, first PCA axis). This variation was explained by difference between heath and meadow habitats; first PCAIV axis shows Polygonaceae separately from other families (middle panel), correlating well with the position of meadow habitat predictor variable along first PCAIV axis (lowest panel).

Subscript figure 6: Eigenvalue of 1st PCA/PCAIV axis, upper row left to right: 0.14, 0.13, 0.15; middle row all plots: 0.03. Ast=Asteraceae, Bet=Betulaceae, Cor=Cornaceae, Cyp=Cyperaceae, Eri=Ericaceae, fer= ferns and allies, Ger = Geraniaceae, Jun=Juncaceae, Pol=Polygonaceae, Poa=Poaceae, Ran=Ranunculaceae, Ros=Rosaceae
$d_i$: distance to centroid for individual $i$

- Individual
- Group centroid