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Isotopic partitioning by small mammals in the subnivium

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Abstract

In the Arctic, food limitation is one of the driving factors behind small mammal population fluctuations. Active throughout the year, voles and lemmings (arvicoline rodents) are central prey in arctic food webs. Snow cover, however, makes the estimation of their winter diet challenging. We analyzed the isotopic composition of ever-growing incisors from species of voles and lemmings in northern Finland trapped in the spring and autumn. We found that resources appear to be reasonably partitioned and largely congruent with phylogeny. Our results reveal that winter resource use can be inferred from the tooth isotopic composition of rodents sampled in the spring, when trapping can be conducted, and that resources appear to be partitioned via competition under the snow.

Introduction

Winter plays a key role in the population dynamics of small herbivorous mammals in the Arctic (Reid and Krebs 1996; Hansen et al. 1999a; Kausrud et al. 2008), but remains a poorly understood period of their annual cycle (Duchesne et al. 2011). Better knowledge of the resource allocations and foraging strategies used by these small mammals during winter is therefore important to improve our understanding of the ecology of these species in arctic food webs (Chappell 1980; Ims et al. 2013; Soininen et al. 2015). Arvicoline rodents (voles and lemmings) are key components of arctic ecosystems, as they constitute the sole prey of secondary consumers during winter (e.g., Ims et al. 2013). Aerial vegetative parts of plants seem to be the main constituents of the vole diet, while lemmings are known to be moss specialists (Stenseth and Ims 1993). It seems that each group of arvicoline shows specific feeding preferences; arvicoline diets would thus expected to be structured according to phylogeny, as has been shown for European rodents (Butet and Delettre 2011).

Flexibility and seasonality in the diets of small arctic mammals have been described to some extent (Hansson 1971a; Hansson and Larsson 1978; Batzli and Henttonen 1990; Eskelinen 2002; Saetnan et al. 2009; Soininen et al. 2009, 2013a). In winter, as small arctic mammals forage in the subnivium (the interface between soil and snow; Pauli et al. 2013; Petty et al. 2015), this task has proven difficult because direct feeding observations and trapping are impossible (but see Bilodeau et al. 2013). Most dietary studies have therefore relied on gut or feces contents of animals trapped between June and September (but see Tast 1974; Soininen et al. 2015), which represent only

snapshots of an individual's summer and autumn diets. So any method that can reconstruct the winter diet from animals trapped when the snow cover is gone would yield valuable information about the ecology of small arctic mammals.

The isotopic composition of an animal's tissue reflects the isotopic composition of the food ingested, shifted through fractionation by a given amount (i.e., discrimination factor), dependent on the animal's metabolism (reviewed by Kohn and Cerling 2002; Cerling et al. 2010; Clementz 2012). In rodents, most studies in isotope ecology have relied on soft tissues or feces (e.g., Sare et al. 2005; Soininen et al. 2014), while stable isotope analyses on teeth have been restricted to reconstructing dietary ecologies in fossil taxa (e.g., Grimes et al. 2004; Hopley et al. 2006; Gehler et al. 2012; Gąsiorowski et al. 2014). Unlike soft tissues, teeth do not decay and, in the case of rodent teeth, are generally conserved unaltered in owl pellets and can thus be used to reconstruct communities over time scales from days to years. Teeth grow progressively and retain the isotopic signal once formed, an interesting property for the study of short-term variations, such as seasonal differences (Dalerum and Angerbjörn 2005). The isotopic composition of tooth tissues corresponds to the diet during the maturation period (Kohn and Cerling 2002). In the case of arvicolines, the ever-growing incisors are completely renewed in 6–8 weeks (Klevezal et al. 1990). Thus, the whole incisor should record the average diet of an individual over a period of 6–8 weeks before death, while the older half of the tooth should represent a signal 6–8 weeks old, but which does not include the last 3–4 weeks. By analyzing this specific part, it should be possible to quantify the April diet (corresponding to the late winter diet, as the snow cover is still present) of rodents trapped in June (when the snow has gone). While this assumption seems logical, there is much uncertainty about metabolic routing and how this affects the isotopic composition of a given tissue (Dalerum and Angerbjörn 2005). So, in order to test the feasibility and robustness of this approach, we selected a sample of voles from Finland with well-studied seasonal ecologies.

In this study, stable carbon and nitrogen isotope analyses were carried out on the lower incisors of specimens from seven species of Finnish arvicolines, belonging to three different tribes, trapped at two separate seasons, in order to test the following hypotheses: (1) the diet of a given species will be closer to that of another species from the same tribe than to that of a species from a different tribe, and (2) it will be possible to infer the winter diet by analyzing the teeth of individuals trapped in spring. Answering these questions will further our understanding of seasonal ecologies in small arctic animals.

Material and Methods

Five *Myodes glareolus* females ("IBH" specimens in Table S1), raised in laboratory conditions, were used to estimate the discrimination factors in isotopic composition between food sources and tooth tissues. From weaning onwards (about 3 weeks after birth), the voles were fed exclusively with breeding diet pellets for rats/mice (number 1314 Fortified; Altromin Spezialfutter GmbH & Co. KG, Lippe, Germany). When sacrificed, all five females were healthy, and between four and 5 months old. The preweaning diet must have been completely overwritten by the postweaning pellet diet at the time of sacrifice, as incisors are completely renewed in 6–8 weeks (Klevezal et al. 1990).

Sixty-two wild arvicolines ("UB" specimens in Table S1) were trapped at two sites in Finnish Lapland. Half of the individuals were trapped in spring (June, $n = 30$), and half in autumn (September, $n = 32$), most of them between 2010 and 2011. The first site, Pallasjärvi, is a boreal taiga zone. The second site, Kilpisjärvi, in the north-westernmost part of Finland, is characterized at higher altitudes by alpine tundra, with subarctic mountain birch forests at lower altitudes, around the biological station. At the Kilpisjärvi site, only the lemmings were trapped in the tundra, while the voles could only be trapped in the forest habitat, which resembles the taiga of Pallasjärvi. Therefore, for subsequent analyses, arvicolines were not separated by trapping locality, but by species, tribe, and season. The specimens analyzed belong to seven arvicoline species (*Microtus agrestis* and *M. oeconomus*; *Myodes glareolus*, *M. rufocanus*, and *M. rutilus*; *Lemmus lemmus* [see Cover image]; and *Myopus schisticolor*) within three tribes (Arvicolini, Clethrionomyini, and Lemmini, respectively). The diets of these species are seasonally variable, species-specific and well known in the Arctic (Table 1).

Samples of plants probably consumed by Finnish arvicolines were collected from Lapland (mostly from Kilpisjärvi; Table S2), in July 2012. The food pellets fed to the laboratory animals were also included in the analyses. We also included reviews by Ben-David et al. (2001) and Drucker et al. (2010, 2012) and reviewed the literature on mosses (see Fig. 1A). The shift from one trophic level to the next is classically thought to be approximately +3‰ in $\delta^{15}N$ (e.g., Ben-David and Flaherty 2012).

The heads of the wild specimens and of the laboratory voles were prepared following the protocol in Appendix S1. As teeth sometimes contain inorganic carbonate, acidification tests were performed. We found that the inorganic carbonate content of the teeth was low enough to have no effect on the carbon and nitrogen isotopic compositions (Appendix S1, Fig. S1). Both lower incisors were extracted from the mandibles. The enamel and dentine of

Table 1. Dietary data from the literature, for the arvicolines studied.

Tribe	Species	Spring/summer diet	Autumn/winter diet	References
Arvicolini	*Microtus agrestis*	Grass/sedge (ca. 50%, up to 80%), forbs (ca. 40%), shrubs (ca. 10%); complemented by invertebrates, bark, berries, fungi	Grass/sedge (ca. 70%, up to 90%), forbs (ca. 15%, up to 65%); complemented by bark, invertebrates, berries, fungi	Hansson (1971a,b), Stenseth et al. (1977), Hansson and Larsson (1978), Saetnan et al. (2009), Butet and Delettre (2011)
	Microtus oeconomus	Grass shoots (ca. 50%, up to 80%), forbs (ca. 20%, up to 65%), horsetail (up to 20%), shrubs (5–10%)	Underground rhizomes and shoots of grass/sedge (up to 95%); complemented by forbs and shrubs	Tast (1974), Batzli and Henttonen (1990), Soininen et al. (2009, 2013a)
Clethrionomyini	*Myodes glareolus*	Forbs (40–50%), invertebrates (30–40%), grass/sedge (ca. 15%, up to 30%), berries (ca. 10%, up to 35%) Complemented by fungi	Forbs (ca. 20%, up to 45%), grass/sedge (ca. 20%), lichen (ca. 20%, up to 35%), fungi (ca. 10%, up to 55%), shrubs (ca. 10%, up to 45%), berries (ca. 10%, up to 25%) Complemented by invertebrates	Hansson (1969, 1971a), Hansson and Larsson (1978), Sulkava (1978, in Viro and Niethammer 1982), Butet and Delettre (2011)
	Myodes rufocanus	Shrubs (ca. 50%, especially *Vaccinium* shoots), forbs (ca. 25%), grass/sedge (ca. 5%), horsetail (ca. 5%)	Shrubs (ca. 60%, especially *Vaccinium*), grass (ca. 15%), forbs (ca. 10%); complemented by *Betula* bark, seeds/berries	Hansson and Larsson (1978), Henttonen and Viitala (1982), Henttonen et al. (1992), Soininen et al. (2009, 2013a)
	Myodes rutilus	Fungi (30–65%), fruits/seeds (10–15%), invertebrates (5–20%), lichen (ca. 10%); complemented by *Vaccinium* shoots	Fungi (ca. 60%), lichen (ca. 25%), fruits/seeds (ca. 10%); complemented by *Vaccinium* shoots	Grodzinski (1971, in Hansson 1985), Henttonen and Peiponen (1982), Bangs (1984)
Lemmini	*Lemmus lemmus*	Moss (ca. 60%, up to 90%), grass/sedge (ca. 20%, up to 80%), dicots (ca. 10%, up to 50%)	Moss (ca. 80%, up to 100%), grass/sedge (ca. 10%)	Koshkina (1961, in Batzli 1993), Tast (1991), Saetnan et al. (2009), Soininen et al. (2013b)
	Myopus schisticolor	Moss (ca. 90%); complemented by leaves	Moss (ca. 90%, up to 100%); complemented by leaves	Bondrup-Nielsen (1993), Eskelinen (2002)

the oldest halves of the incisors (which had formed at least 3–4 weeks before trapping; Klevezal et al. 1990) were manually ground into a fine homogeneous powder, with a mortar and pestle. The resulting powder was then dried overnight at 60°C. All plant samples were frozen (−75°C) for at least 24 h, then lyophilized (<1.5 mbar, −132°C) for at least another 24 h, and then ground to a fine powder. All the plant and pellet samples were dried overnight at 60°C, the day before the preparation of the tin capsules.

Three tin capsules per individual (arvicolines, plants and pellets) were analyzed for elemental carbon and nitrogen proportions and for stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopic compositions. Isotopic compositions are expressed relative to the conventional standards, Vienna Pee Dee Belemnite (VPDB) for carbon (Craig 1953) and atmospheric N_2 for nitrogen (Mariotti 1983). To calibrate the elemental and isotopic analyses, a glutamic acid standard (L-USGS 40: C = 40.8%, N = 9.5%, $\delta^{13}C = -26.389 \pm 0.042‰$, $\delta^{15}N = -4.5 \pm 0.1‰$) was used. The precision of analysis was $\pm$ 0.15‰ ($\delta^{13}C$) and $\pm$ 0.2‰ ($\delta^{15}N$). The values for the three tin capsules per individual were averaged before analysis. The variation between these three samples did not exceed the precision of analysis.

Interspecific and seasonal dietary variations were tested. An unsupervised model-based classification (Gaussian finite mixture model, fitted by an expectation–maximization algorithm; Fraley and Raftery 2002; Fraley et al. 2012) was run on the wild voles, to test for a grouping based on the isotopic composition of the teeth. The optimal model was chosen according to the highest Bayesian information criterion. The magnitude of the agreement between this classification and the known heterogeneities existing in the sample (taxonomy and season) was then calculated using Cohen's Kappa statistic (Cohen 1960). A two-way ANOVA with type II sums of squares was performed on each stable isotope ratio. A square root transformation on the $\delta^{15}N$ values, $\sqrt{(\delta^{15}N + 1)}$, was required prior to statistical analysis. The factors were tribe, species nested within tribe, and season; all interactions between these factors were also tested. As the sample size was in some cases quite small, the species factor

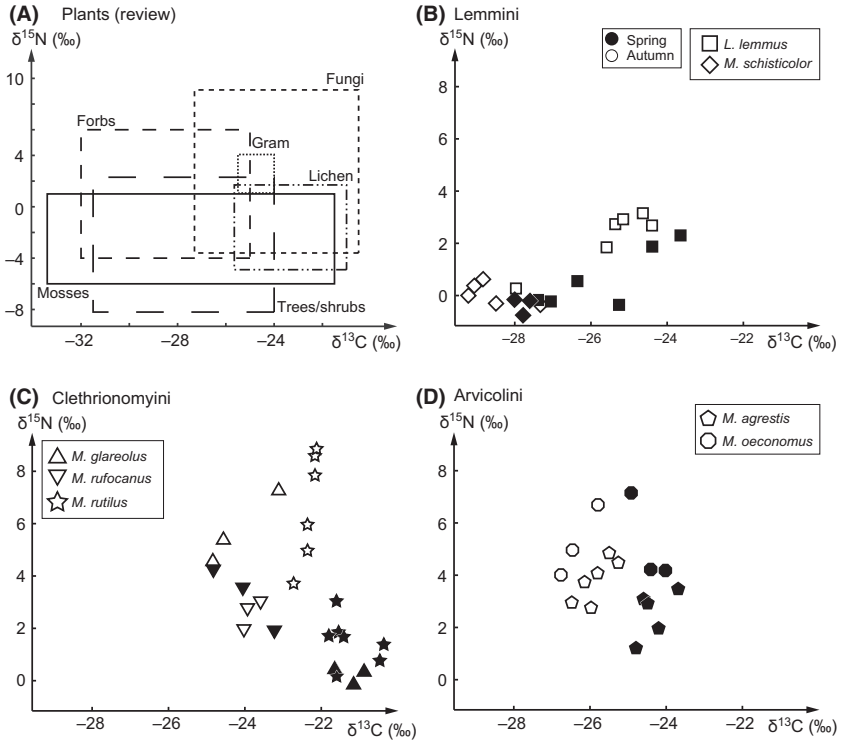

Figure 1. (A) Review of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopic compositions (in ‰) of plant types. The ranges for mosses are based on Nadelhoffer et al. (1996), Brooks et al. (1997), McLeman (2006), and Loisel et al. (2009). Ranges for other plant types are summarized from Ben-David et al. (2001) and Drucker et al. (2010, 2012). gram = graminoids. (B–D) Carbon and nitrogen isotopic compositions of the teeth studied. Black symbols for specimens trapped in spring; white symbols for autumn. (B) Lemmini: *Lemmus lemmus* (squares) and *Myopus schisticolor* (diamonds). (C) Clethrionomyini: *Myodes glareolus* (upright triangles), *M. rufocanus* (inverted triangles) and *M. rutilus* (stars). (D) Arvicolini: *Microtus agrestis* (pentagons) and *M. oeconomus* (octagons). Note that (A) and (B–D) are not drawn in the same isotopic space.

was not tested alone. The significance of interesting linear contrasts between groups was assessed using pairwise *t*-tests with a Welch correction for heteroscedasticity and a Holm correction on the *P*-values. These contrasts were as follows: the mean differences between any two tribes, the mean differences between any two species of the same tribe, and the seasonal differences within a tribe. Even though mixing models in general, and Bayesian mixing models in particular, are often used (Wolf et al. 2009; Newsome et al. 2012; Phillips 2012), it was not possible to apply them to this dataset (see Appendix S2 for details). The open-source software R 3.1.0 (R Development Core Team 2014) was used with the following packages: car (Fox and Weisberg 2011), doBy (Højsgaard et al. 2013), irr (Gamer et al. 2012), mclust (Fraley et al. 2012), R.utils (Bengtsson 2014), RSvgDevice (Luciani et al. 2014), and xlsx (Dragulescu 2013).

Results

The five laboratory specimens show very little deviation from the mean, lower than any of the other populations (Table S3). The discrimination factors (the difference between the isotopic composition of the teeth and that of the food sources) are $\Delta^{13}C_{tooth\text{-}food} = +2.40 \pm 0.13‰$ and $\Delta^{15}N_{tooth\text{-}food} = +6.01 \pm 0.16‰$ (Fig. S1). These values fall within the ranges of discrimination factors in hairs and bone collagen published for voles (see Appendix S2). The carbon and nitrogen compositions of plants in northern Finland are given in Table S2. Our plant samples from Lapland have isotopic compositions that fall within the ranges of published data from northern America (Fig. 1A).

The unsupervised classification (cluster analysis) grouped the isotopic data into four clusters (Fig. 2A), based on taxonomic affinity and season, although there is some overlap (Fig. 2B). The agreement between clustering and taxonomy plus season is significant (Cohen's Kappa: $\kappa = 0.537$, $P < 0.001$), with the fourth cluster probably lowering the κ value. The clustering into tribes (plus season) is also supported by the two-way ANOVA, where the tribe effect is significant ($\delta^{13}C$: $F = 155.26$, $P < 0.001$ and $\delta^{15}N$: $F = 54.41$, $P < 0.001$). The six contrasts between tribes show that each tribe differs from the other two (Table S4). There are also significant differences between species within each tribe (effect of species nested within tribe for $\delta^{13}C$: $F = 21.12$, $P < 0.001$ and for $\delta^{15}N$: $F = 8.61$, $P < 0.001$; Fig. 1B–D, Tables S3–S4).

Both the seasonal effect ($\delta^{13}C$: $F = 24.89$, $P < 0.001$ and $\delta^{15}N$: $F = 56.55$, $P < 0.001$) and the interaction between tribe and season ($\delta^{13}C$: $F = 4.07$, $P = 0.023$ and $\delta^{15}N$: $F = 8.01$, $P < 0.001$) are significant. The interaction between species (nested within tribe) and season is also significant ($\delta^{13}C$: $F = 3.47$, $P = 0.014$ and $\delta^{15}N$: $F = 7.28$, $P < 0.001$). The large seasonal differences observed between animals trapped in spring and their autumn

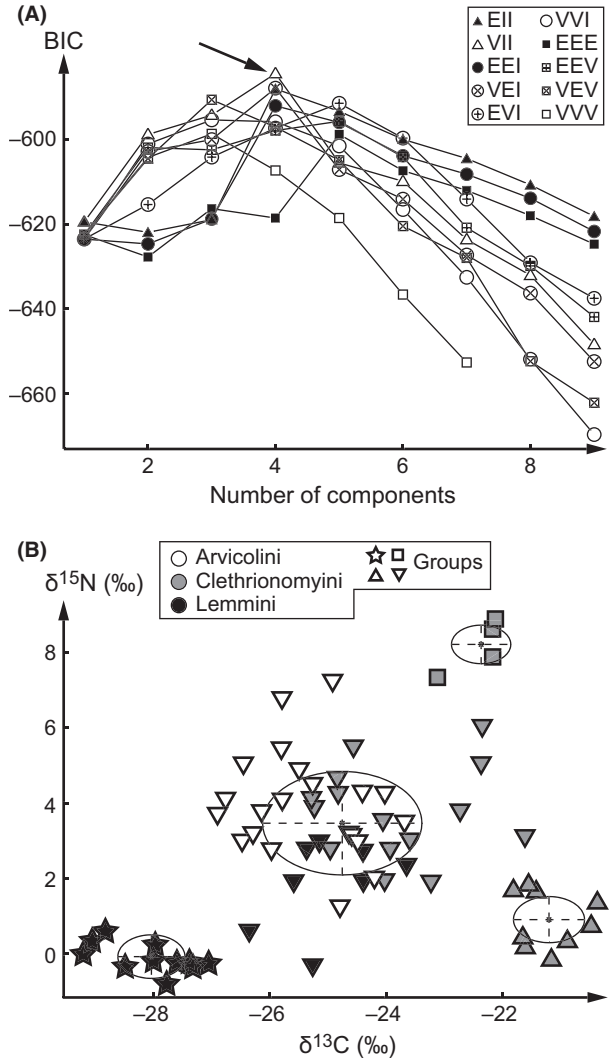

Figure 2. Unsupervised model-based classification. (A) Bayesian information criterion (BIC) relative to the number of components (i.e., clusters) tested by each model. The arrow highlights the best model (highest BIC): spherical variance–covariance matrices and varying volume (model VII, white triangles) with 4 components. (B) Clustering of each arvicoline tooth sample according to the unsupervised classification (symbols), with taxonomic affinities identified by gray shading. The samples are shown in the carbon (δ^{13}C) and nitrogen (δ^{15}N) isotopic space of arvicoline incisors.

counterparts (Fig. 1B–D, Table S3) are driven solely by Arvicolini on δ^{13}C (+1.6‰ from autumn to spring), and by Clethrionomyini on δ^{15}N (−3.8‰ from autumn to spring) (Table S4). Testing for these seasonal contrasts within each tribe will require additional samples, so interspecific seasonal differences are only described qualitatively here. There are marked increases (1–3‰) in δ^{13}C in spring in species of both Arvicolini and Clethrionomyini (Fig. 1C–D). Additionally, a very large decrease in δ^{15}N (approximately 5‰) is observed in spring in *Myodes glareolus* and *M. rutilus* (Fig. 1C).

Discussion

Our isotopic data reveal that each tribe has a specific diet, sometimes modulated by seasonality, thus extending the hypothesis that diet is structured according to phylogeny (Butet and Delettre 2011) to include Arctic arvicolines. Lemmini have very specialized diets based on mosses, where δ^{13}C values span a very large range, but are generally the lowest of all plant types (Nadelhoffer et al. 1996; Brooks et al. 1997; McLeman 2006). The more negative position of Lemmini in the isotopic space is consistent with this diet. The higher proportion of graminoids, fungi, lichen, and invertebrates in the diets of Arvicolini and Clethrionomyini than in that of Lemmini explains the higher δ^{13}C and δ^{15}N values in these two tribes. Clethrionomyini have the highest δ^{13}C values, consistent with their substantial consumption of fungi and lichens.

Within Lemmini, the higher values for both isotopes (δ^{13}C and δ^{15}N) in *L. lemmus* can be explained by the fact that it is less dependent on mosses than *M. schisticolor*, consuming more graminoids to complement its diet. Within Arvicolini, the higher δ^{15}N values of *M. oeconomus* compared to *M. agrestis* seem to contradict the dietary data available in the literature, as *M. oeconomus* consumes only green plant parts (generally low δ^{15}N, but higher values for horsetail, for example), while *M. agrestis* may include some invertebrates and fungi (high δ^{15}N) in its diet. Within Clethrionomyini, *M. rutilus* has higher δ^{13}C values than *M. rufocanus*, consistent with its greater consumption of fungi and lichens (high δ^{13}C). High δ^{15}N values were expected for *M. glareolus* and *M. rutilus*, based on their consumption of fungi and invertebrates. The broad range of δ^{15}N values observed in these species could result from two complementary factors: (1) the low δ^{15}N values of lichen partially compensate for the high values of fungi and invertebrates and (2) the proportions of lichens, fungi, and invertebrates are seasonally very variable, and therefore, average values are somewhat artificial.

The isotopic composition of ever-growing rodent incisors can be used to assess the isotopic composition of the diet, with a delay of one to 2 months. We found no sign of isotopic seasonality in Lemmini, consistent with their constant reliance on mosses and with observed food storage behavior (Eskelinen 2002). In contrast, seasonality was recorded in both Arvicolini and Clethrionomyini. Arvicolini rely more on graminoids, at the expense of forbs and shrubs, in winter. The winter diet should therefore have a higher carbon isotopic composition. Individuals trapped in spring do indeed have higher δ^{13}C values

than autumn specimens, thus reflecting their winter diet. *Microtus agrestis* and *M. oeconomus* are known to show interference competition in summer, favoring the latter (Henttonen et al. 1977). Coexistence is thought to be linked to relaxed competition in winter, when *M. oeconomus* shows a higher level of individual activity than *M. agrestis* (Hoset and Steen 2007). Stable isotopes also suggest resource partitioning during winter, as *M. oeconomus* seems to have higher δ^{15}N values. Alternatively, the greater activity of *M. oeconomus* in winter, despite potential food shortage, may result in nutritional stress. This may induce impaired nitrogen balance, leading to higher δ^{15}N values unrelated to any change in food supply (Fuller et al. 2005; Petzke et al. 2010). As the lighter isotope is preferentially excreted and not replaced by external sources when the organism is fasting, protein synthesis during tooth renewal should lead to an increase in δ^{15}N (Vanderklift and Ponsard 2003; Martínez del Rio et al. 2009; Lee et al. 2012). *Myodes rufocanus* is close to Arvicolini, in the isotopic space, but without any perceptible seasonal shift. Its winter signature is very similar to that of *M. agrestis*, suggesting that some resource competition occurs. This observation is in agreement with the over-winter population dynamics of *M. rufocanus*, related to the size of the vole community (Hansen et al. 1999b). The winter diets of *M. glareolus* and *M. rutilus* include fewer or no invertebrates (high δ^{15}N), but more lichens (low δ^{15}N, high δ^{13}C), most likely because of food availability, and should thus result in lower δ^{15}N but higher δ^{13}C values. These species indeed show a marked decrease in δ^{15}N and an increase in δ^{13}C between animals trapped in autumn and those trapped in spring. Interestingly, resource use between these two closely related species, which produce viable F1 individuals (Grant 1974) and present mtDNA introgression (Boratyński et al. 2014), seems closer in winter than in summer, suggesting probable resource competition under the snow. Stable isotope analysis suggests strong resource partitioning between these species and *M. rufocanus*. This is in agreement with the suggested absence of competition between *M. rufocanus* and *M. rutilus* (Mal'kova and Yakimenko 2007).

The present study is, to our knowledge, the only ecological analysis of carbon and nitrogen isotopes from rodent teeth (see Gąsiorowski et al. 2014 for palaeoenvironmental reconstructions). It is also the only study on isotopic ecology based on the teeth of small arctic mammals. We show that food resources are partitioned among arvicoline tribes and species. By analyzing only the apical part of ever-growing incisors, it is possible to access the late winter diet of arvicolines trapped in June, when the snow cover is gone, thus bringing to light resource use of this key guild in the Arctic food web. This methodology could be used on other rodent species, and in other contexts where observations and trapping are difficult during certain periods. This approach also opens up the possibility of using stable isotope analysis on pellets to track the ecology of both rodents and birds of prey.

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Conflict of Interest

The authors declare no conflict of interest.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Carbon (δ^{13}C) *vs.* nitrogen (δ^{15}N) isotopic compositions (in ‰) of the food pellet (grey triangle), and of laboratory vole teeth before (white dots) and after (black dots) decarbonation with HCl. Dotted lines connect samples before and after HCl treatment.

Table S1. Information about the specimens studied: tribe (following Robovský et al. 2008); species; inventory number (ID); trapping locality, season and year; carbon (δ^{13}C) and nitrogen (δ^{15}N) isotopic compositions (in ‰), and carbon ([C]) and nitrogen ([N]) elemental compositions (in %) of the teeth studied.

Table S2. Information on the food samples studied: species; sampling locality; part of plant analysed; carbon (δ^{13}C) and nitrogen (δ^{15}N) isotopic compositions (in ‰), carbon ([C]) and nitrogen ([N]) elemental compositions (in %), and carbon to nitrogen ratio (C:N = [C]/[N]).

Table S3. Mean and standard deviation (SD) of the carbon (δ^{13}C) and nitrogen (δ^{15}N) isotopic compositions (in ‰) of the arvicoline teeth studied.

Table S4. Results of the pairwise *t*-tests (df: degree of freedom, *P*: *P* value, *t*: *t*-statistics).

Appendix S1. Details of the method: preparation of arvicoline heads and pre-treatment.

Appendix S2. Bayesian mixing models and discrimination factors.