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FACULTY OF BIOSCIENCES, FISHERIES AND ECONOMICS
DEPARTMENT OF ARCTIC AND MARINE BIOLOGY

Interactions between small rodents and their food plants in tundra habitats

Eeva Marjatta Soininen

A dissertation for the degree of
Philosophiae Doctor

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Supervisors

Professor Rolf A. Ims
Professor Nigel G. Yoccoz
Associate professor Kari Anne Bråthen

Department of Arctic and Marine Biology
University of Tromsø
NO-9037 Tromsø, Norway

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Oikos, in press, doi: 10.1111/j.1600-0706.2012.20689.x

Abstract

Small rodents are key herbivores of arctic ecosystems, where their cyclic population dynamics have important implications for vegetation dynamics. The role of vegetation for shaping small rodent population dynamics remains, however, unclear. Evaluation of this interaction has been greatly hampered by the rather fragmentary knowledge of small rodents feeding ecology, which in turn is due to methodological challenges in studying small rodent diets. In this thesis, I investigated interactions between small rodents and vegetation, focusing on variability of both diets and plant defences induced by rodent herbivory.

In order to overcome limitations set by methods, I have evaluated the use of two recently developed methods and one traditionally used method for studying small rodent diets (papers I, II and IV). I found that novel DNA metabarcoding methods give the best taxonomic resolution whereas traditional microhistological methods may still be useful to elucidate which plant parts have been eaten. Moreover, use of stable isotope analysis in research of small rodent feeding habits can be useful when evaluating the temporal persistence of diets.

In three observational studies (papers II, III and IV) I described diets of small rodents in tundra habitats and assessed sources of variability in them. I found that diets of my study species were more diverse than previously believed, suggesting that diversity is an important but previously underrated trait of small rodent diets. Nutritional quality seems to determine which food items are preferred, as small rodents selected in general for most palatable food items. In addition to nutritional drivers, my results suggest that various ecological drivers, such as food availability, competition and predation risk avoidance, are important determinants of for small rodent diets in the wild. A better incorporation of ecological and nutritional drivers into a common framework is therefore needed to understand what shapes diets of small rodents, and herbivores in general, in natural habitats.

I evaluated the impact of herbivory on grass silica defences in an experimental study (paper V). I found that levels of such defences vary between locations, probably due to heritable differences among grass populations in the response to herbivory and differences in local growth conditions. Based on such spatial variation and the large proportion of other food items included in the diets of the focal small rodent populations, it is unlikely that silica-based defences would have a strong direct role in shaping small rodent population dynamics in Finnmark. However, increased levels of silica in grasses reduce grass palatability for rodents, and hence probably impact rodent diet quality indirectly, through a shift to diets with less grasses. I therefore suggest that availability of alternative food items is likely to be an important factor shaping the interaction between small rodents and grasses.

Variability in both small rodent diets and plant defences suggests that interaction between vegetation and a small rodent species may show pronounced spatial variation. This, together with my findings on the diversity of diets and its increase during high population densities, indicates that a single plant defence mechanism is unlikely to shape rodent-vegetation interactions. I suggest that deeper understanding of the role of food for small rodent population dynamics could rather be gained by focusing on the compensatory nutritional effects of different food items as well as diet diversity.

Introduction

Small rodents in tundra food webs

Terrestrial tundra food webs are characterized by low productivity and diversity of both plants and animals (Batzli et al. 1980; Krebs et al. 2003; Ims and Fuglei 2005). This relative simplicity, in comparison to more southern food webs, makes them appropriate study systems for trophic interactions. In tundra food webs, small rodents form a central link between vegetation and predators, as most of the transformation of plant biomass to animal biomass happens through them (Batzli et al. 1980; Krebs et al. 2003; Ims and Fuglei 2005; Gauthier et al. 2011; but see Legagneux et al. 2012). Even in tundra ecosystems which have other herbivores, these are usually not equally available for predators. Biomass of the other important mammalian herbivores, reindeer (*Rangifer tarandus*) and musk oxen (*Ovibos moschatus*), is low in many parts of the arctic (Jefferies et al. 1994; Batzli et al. 1980), or extensively used up by humans as is the case for Fennoscandian semi-domesticated reindeer. On the other hand, herbivorous birds, especially geese, are locally an important trophic link (Jefferies et al. 1994; Gauthier et al. 2011), but their presence is restricted to summer season and particular locations.

Most arctic small rodent populations undergo cyclic high amplitude changes in population density (Ims and Fuglei 2005; Oksanen et al. 2008), which tend to characterize whole tundra food webs. During population peaks, small rodent herbivory affects plant biomass (Andersson and Jonasson 1986; Hambäck et al. 2004; Olofsson et al. 2012), vegetation composition (Andersson and Jonasson 1986; Moen et al. 1993; Olofsson et al. 2004; Ravolainen et al. 2011; Villareal et al. 2012), plant mortality (Ravolainen et al. *in revision (b)*) and reproduction (Andersson and Jonasson 1986; Oksanen and Ericson 1987). Periodic heavy grazing by small rodents seems to even have the potential to maintain alternative stable states of tundra vegetation communities (Virtanen et al. 1997; Villareal et al. 2012).

In addition to vegetation, small rodent population dynamics affect the predators of tundra food webs. Tundra predators respond to fluctuations of food availability, i.e. rodent densities, both functionally and numerically (Batzli et al. 1980; de Korte and Wattel 1988; Elmhagen et al. 2000; Gilg et al. 2003; Killengreen et al. 2011). Rodent population dynamics have even indirect consequences for species which represent alternative prey for tundra predators. For example, during years of low rodent population density the reproduction success of ground-breeding birds is low whereas their mortality is high (Bêty et al. 2001; Sittler et al. 2000; Gauthier et al. 2004).

Rodent population dynamics and vegetation

"However, anyone who is familiar with the literature on microtine cycles knows that it does not lack reasonable hypotheses. If only they were all easily testable, perhaps we could more confidently explain the perplexing population fluctuations of voles"
G. O. Batzli and F. A. Pitelka, 1975

Interactions between arctic small rodents and vegetation have been mostly studied in the context of rodent population dynamics. A range of hypotheses on how rodent-vegetation interactions may, alone or together with other factors, cause cyclic population dynamics have been put forward. These hypotheses suggest that small rodent population densities are either affected directly by plant productivity cycles or by a feed-back mechanism of changes in vegetation caused by small rodents themselves.
While plant productivity cycles seem to have no clear correlation with rodent population dynamics (Andersson and Jonasson 1986; Oksanen and Ericson 1987; Olofsson

Box 1. Terminology

Plants:

plant defence - A plant defence mechanism against herbivores or other stressors. Such defence can either be chemical, such as many toxic secondary metabolites, or morphological, such as spikes, woody structures etc.

induced defence - A plant defence mechanism against herbivores or other stressors, which is only expressed after a stimuli of such a stressor.

constitutive defence - A plant defence mechanism against herbivores or other stressors, which is expressed independently of the presence of such stressors.

tolerance - A plant strategy against herbivory, alternative to defence. Plant that tolerates herbivory does not defend itself in order to avoid herbivory, but is able to compensate the lost tissues after herbivory without a notable cost.

palatability - Attractiveness of a food item to a consumer. A combined measure of sensory inputs such as taste, odor, texture and post-ingestive effects of nutrients and defence compounds.

plant functional group - A group of plants which are characterized by similar functional traits, not necessarily taxonomically related. Traits such as growth form (woody/herbaceous, evergreen/deciduous), nitrogen uptake (hemiparasite/legume) or decomposability can be used to characterize a plant functional group.

Herbivores:

generalist - A herbivore feeding on a wide range of food items.

specialist - A herbivore feeding on a single food item or a narrow range of food items.

trophic niche - An animals niche defined by the range of food items it consumes.

absolute food preference - An animals preference for a food item independent of whether it is available or not.

realized food preference - Food preferences that are conditioned on the prevailing ecological circumstances, such as the available species pool, and defined as ingested proportions being higher than those available in vegetation.

et al. 2012), considerable uncertainty about the role of feed-back mechanisms still exists (Klemola et al. 2003; Oksanen et al. 2008; Krebs 2011). This group of hypotheses is based on the logic that an increasingly dense rodent population has an increasing impact on its food sources. At high population densities the availability of food, or the availability of good quality food, may become insufficient to fulfill the needs of all rodent individuals. This is assumed to either decrease reproduction or increase mortality, and as a consequence population densities should diminish. The increasing impact of rodents on their food sources may, moreover, cause plants to induce various defences. This, in turn, should further reduce food quality for rodents, reducing their health status, and thus accentuate the consequences for population density. Finally, vegetation may need several years to recover from a rodent population peak, potentially causing the delayed feed-back needed to produce interaction cycles.

The suggested feed-back hypotheses can be divided into two types, based on what small rodents are expected to feed during the population peaks. First, the biomass of preferred food plants has been suggested to diminish to low levels during high rodent population densities, forcing them to shift to less preferred food plants of lower quality; i.e. plants with less nutrients, more defence compounds or even lethal toxins (Schultz 1964; Freeland 1974; Plesner Jensen and Doncaster 1999; Berg 2003). The second group of feed-back hypotheses is based on preferred food plants being eaten throughout population cycles. As a consequence of heavy grazing during high population densities, these plants are suggested to either induce defences or decrease in nutrient content (Laine and Henttonen 1983; Lindroth and Batzli 1986). This group of hypotheses has been evaluated by several authors who have studied various plant defence mechanisms, such as phenolics (Lindroth and Batzli 1984; Harju and Hakkarainen 1997), proteinase inhibitors (Seldal et al. 1994; Bråthen et al. 2004; Lindgren et al. 2007) and silica-based defences (Massey and Hartley 2006; Massey et al. 2008).

Nevertheless, current knoweldge on small rodent diet changes during population density fluctuations is relativly limited. While grazing signs of small rodents on poorly palatable food have been found to increase with population density (Hansson 1986), it remains unclear whether this is simply caused by the larger number of small rodents or whether small rodent diets actually change. Moreover, the few studies evaluating changes of small rodent diets during population density changes have rendered contrasting conclusions. While Batzli and Pitelka (1975) could not relate population density to changes in diets, Bergeron (1980) and Larsson and Hansson (1977) suggest that lower quality food items are more frequently consumed during population density peaks. Hence, proper evaluation of the assumptions of any of the hypotheses stating that vegetation has an impact on small rodent population dynamics requires knowledge that is currently lacking. Most importantly, what are the food plants used by different rodent species and populations during population density peaks? To what extent these plants have defence mechanisms, constitutive or induced?

Grass silica defences

Grasses have long been considered to cope with herbivory mainly by tolerating it (Vicari and Bazely 1993), and therefore only recently grass defences against herbivores have been suggested to play a role in plant-herbivore interactions. Nevertheless, grasses do have a range of defence mechanisms, of which silica-based defences are among the most important (Vicari and Bazely 1993). Silica-based defences of grasses have experimentally been shown to be induced by vole herbivory, deter feeding by voles and reduce digestibility for them (Massey and Hartley 2006; Massey et al. 2008). Furthermore, the silica levels of grasses have been found to follow vole population dynamics in the wild (Massey et al. 2008). Based on these findings, Massey and co-authors have proposed that grass silica defences may be driving vole population cycles (Massey and Hartley 2006; Massey et al. 2008).

This hypothesis has been developed using a temperate forest ecosystem as a study model (Massey et al. 2008). However, grass silica defences have been found to be induced by grazing also elsewhere, notably in ecosystems characterized by grazing, such as savannas and prairies (McNaughton et al. 1985; Brizuela et al. 1986; Cid et al. 1989). Moreover, Cooke and Leishman (2011) suggested that silica plays a bigger role in plant ecology than previously believed. Fennoscandian tundra vegetation is heavily grazed by semi-domesticated reindeer, which seems to increase biomass of silica-rich grass species (Moen and Danell 2003; Ravolainen et al. 2011). Grass silica defences can therefore be expected to play a yet unknown role for plant-herbivore interactions in Fennoscandian tundra habitats.

Food selection by small rodents

Herbivore food selection has long been studied as function of plants nutritional quality (see "*nutrient constraint hypothesis*" by Westoby 1978 and "*detoxification limitation hypothesis*" by Freeland & Janzen 1974). However, plant nutritional quality for a herbivore is a complex measure, consisting of gained energy and nutrients as well as the negative effects of plant defences. Consequently, the nutritional value of a food item for a herbivore depends on the interplay of its different contents, as well as the abundance and quality of other concurrently available food items (Belovsky and Schmitz 1994; Dearing et al. 2000; Behmer et al. 2002; Provenza et al. 2007; Lisonbee et al. 2009; Nersesian et al. 2012b; Pretorius et al. 2012). Until recently, most research has been based on either nutrients or plant defence compounds alone, and the understanding how these two interact and together define palatability is still developing (Dearing et al. 2000; Behmer et al. 2002; Provenza et al. 2007).

Small rodents have been experimentally shown to avoid a range of compounds present in plants, such as phenolics, alkaloids, silica and acid detergent fiber (ADF) (Lindroth and Batzli 1984; Bergeron and Jodoion 1987; Harju and Hakkarainen 1997; Massey et al. 2006). They have also been shown to prefer foods with higher protein content (Bergeron and Jodoion 1987; Harju and Hakkarainen 1997). Still, some studies found no effect of food quality on food selection by small rodents (Bélanger and Bergeron 1987; Pedersen et al. 2011), while others indicate that palatability is an important food selection criteria (Batzli and Jung 1980; Harju and Hakkarainen 1997). This diversity of results is unsurprising, as the biochemical diversity of a plant community is likely to have diverse effects on small rodents food selection. For example, plant defence compounds differ in terms of the amounts of nutrients required for their detoxification. Consequently, the impact of a plant defence compound on herbivore feeding behaviour depends on the chemical composition of the other components of the herbivores diet (Behmer et al. 2002; Villalba et al. 2002). Moreover, the impacts of a plant defence compound differ between small rodent species (Batzli and Jung 1980; Lindroth et al. 1986), and results from one rodent species can therefore hardly be extrapolated to apply all species.

Still, feeding behaviour of small rodents in the wild is affected by a range of other factors than "simply" choosing a meal from the chemical landscape. Another main branch of research on herbivore food selection has been focused on optimal selection of food items or feeding patches based on their costs and benefits. Studies within this body of research have evaluated the impacts of various ecological drivers, such as food availability, predation avoidance and competition on herbivore food selection (Senft et al. 1987; Brown 1988; Ripple and Beschta 2004; Searle et al. 2008; Tuft et al. 2011). This framework leans mainly on theories which originally emerged to explain predator food selection, such as the "*optimal foraging theory*" by MacArthur and Pianka (1966) and "*marginal value theorem*" by Charnov (1976). These studies therefore mostly use a simple currency to measure the value of food items, such as energy or total nitrogen, or use herbivores preference as an index of food quality. Consequently, integrated understanding of ecological and nutritional drivers of herbivores food selection is poorly developed.

For small rodents, increased availability of a food item has been shown to increase its use, although it is unclear what regulates this relationship (Batzli et al. 1981; Gross et al. 1993; Lundberg 1988; Hobbs et al. 2003) and what is the impact of alternative food item availability (Pusenius et al. 2003). However, variability of small rodent diets between habitats, albeit poorly known for most species, indicates that food availability often has an impact on diets (Batzli and Pitelka 1983; Batzli and Henttonen 1990; Tast 1991). It has also been established that predation risk affects both small rodent habitat selection, in terms of opting for more sheltered habitats, and the time invested on feeding (Hambäck et al. 1998; Ylönen & Brown 2008). Little direct evidence exists on the impacts of competition on small rodents food selection. Still, decreased survival and reproduction as a result of food competition (Huitu et al. 2003) indicates that also competition is an important factor in determining what small rodents feed on. Even so, the interplay between various bottom-up (plant chemistry, quantity and spacing), top-down (predation risk) and ”sideways” (competition) drivers on small rodent food selection is poorly understood. An evaluation of the relative importance of these different drivers in wild is one of the first steps needed towards an integrated understanding of small rodent food selection.

Diets of tundra-dwelling small rodents

Many of the above outlined gaps in the understanding of interaction between small rodents and vegetation are caused by a lack of knowledge on rodent diets in the wild. This, again, is mainly due to lack of methods which could have provided data at appropriate depth (i.e. taxonomic resolution) and width (i.e. across relevant spatial and temporal scales). Three methods have traditionally been available for evaluating the food habits of small rodents, namely studies on stomach contents, cafeteria experiments and observations of grazed vegetation. The two latter are valuable methods to study rodent-plant interactions, but fail to answer a fundamental question: what is the composition of small rodent diets in their natural habitats? On the other hand, studies of stomach contents using microhistological methods are challenging to conduct. Such methods are time-consuming and require often extensive work on constructing a reference-database and training observers. The plant epiderm fragments found in small rodent stomachs are often very small, only a few cells, implying that they can often be identified only at a coarse taxonomic resolution. In addition, observers are likely to have a different threshold in identifying a fragment to an identifiable group *versus* classifying it as unidentifiable. To conduct a microhistological study therefore requires investing a great amount of work to a project which may result in a coarse description with potential biases between observers. Despite these challenges, adequate knowledge for general descriptions of small rodent diets has been gained. Below, I summarize what is known about the diets of the primary study species of this thesis; grey-sided vole (*Myodes rufocanus*), tundra vole (*Microtus oeconomus*) and Norwegian lemming (*Lemmus lemmus*), based on studies published prior to this thesis.

Myodes rufocanus

Diet of the grey-sided vole (Figure 1), has been investigated by observations of feeding signs in subarctic birch habitat (Kalela 1957) as well as stomach contents from forested habitats (Hansson 1969; Hansson and Larsson 1978). Together, these studies indicate that grey-sided voles feed on *Vaccinium* shrubs, herbs and grasses in summer, with an increased use of shrubs in wintertime. At the same time the studies disagree in many aspects; while Hansson (1969) and Hansson and Larsson (1978) conclude that grasses, especially *Avenella flexuosa*, and mosses are frequently eaten, Kalela (1957) claims that this is not the case. While such discrepancy indicates that grey-sided vole diets

Figure 1: Grey-sided vole, *Myodes rufocanus*

may differ between areas and habitats, it is also possible that the different conclusions depend on the method used. Similar indication of variable diets between seasons and regions is given by the studies conducted in Japan, where the species mainly feeds on leaves and shoots of bamboo in winter but also on various forbs and grasses during summer (Kaneko et al. 1998). To my knowledge, no published studies evaluate the diets of grey-sided voles in tundra habitats. However, several experiments on the effect of grey-sided voles on *Vaccinium myrtillus* have shown that it is an important forage species for grey-sided voles above the treeline (Hambäck and Ekerholm 1997; Dahlgren et al. 2007, 2009).

Microtus oeconomus

Tundra vole (Figure 2) feeding habits have been investigated based on stomach contents in Finland (Tast 1974) and Alaska (Batzli and Jung 1980; Batzli and Henttonen 1990). The animals sampled by Tast (1974) were trapped in the subarctic birch zone, although no details of habitats were included. Both Alaskan studies focus on open tundra habitats; Batzli and Jung (1980) trapped tundra voles mainly in graminoid-dominated wet tundra while Batzli and Henttonen (1990) compared diets along a moisture gradient. These studies agree that monocotyledons, especially *Eriophorum*, form the bulk of the tundra voles diet. In addition, both Tast (1974) and Batzli and Henttonen (1990) indicate that during summer both horsetails (*Equisetum*) and herbs were eaten, whereas Batzli and Jung (1980) found that also willows (*Salix* sp.) were an important component of tundra vole diet. Moreover, Batzli and co-authors indicate that tundra vole feeding habits do not vary greatly between different habitats (Batzli and Henttonen 1990; Batzli and Jung 1980). In addition to stomach content studies, tundra vole food preferences have been investigated in a cafeteria experiment using voles originating from a Polish population (Gebczyńska 1970). In this study, voles were found to preferably select for various forbs, although they were not offered *Eriophorum*, as it was not available for tundra voles in the studied population. Differences between these studies suggest that food habits and potentially also food preferences of tundra voles may differ based on the available food.

Figure 2: Tundra vole, *Microtus oeconomus*

Figure 3: Norwegian lemming, *Lemmus lemmus*

Lemmus lemmus

Studies on the feeding habits of the Norwegian lemming (Figure 3) are more abundant than those of tundra-dwelling voles. Their diets have been investigated using microhistological analysis of stomach contents (Koshkina 1961; Hansson 1969; Tast 1991; Saetnan and Batzli 2009), and faeces (Stoddart 1967), as well as feeding trials (Kalela et al. 1961). In general, all of these studies agree on the main pattern; Norwegian lemmings feed mainly on mosses and monocotyledons. However, there are several discrepancies between the studies. For example, lemmings have been claimed to select for mosses (Kalela et al. 1961) and select against them (Saetnan and Batzli 2009). Different mosses have been suggested to be the most important ones; *Hylocomnium splendens* (Hansson 1969) and *Dicranum* sp. (Kalela et al. 1961; Koshkina 1961). Some authors have done an impressive effort analysing a large sample size (Koshkina 1961; Tast 1991), providing possibilities to evaluate temporal and spatial trends in lemmings food habits. Based on these studies, the use of mosses seems to decrease during summer, with a simultaneous increase in the use of grasses (Kalela et al. 1961; Koshkina 1961; Tast 1991). Findings on spatial variation in lemming diets are less consistent. On one hand, Tast (1991) and Saetnan and Batzli (2009) studied lemming diets in similar habitats, namely alpine meadows with scattered willow thickets, but found rather different diets. On the other hand, the comparison of diets between different habitats by Tast (1991) indicates that such differences are small. Several aspects of Norwegian lemming diet, such as the identity of important food species and the extent and causes of spatial variation, remain thus unclear.

Aims

My general aim with this thesis was to describe and assess sources of variability in interactions between small rodents and vegetation. Specifically, my **first** aim was to describe what small rodents on subarctic tundra eat, using new methodology (papers I, II, III). My **second** aim was to evaluate different methods which could be used to study small rodent diets, taking advantage of their strengths but correcting for their biases (papers I, II, IV). **Third**, I intended to use the new on knowledge small rodent diets to investigate why they eat what they eat. To do this, I aimed to combine data on the availability of different food items as well as on competition to better understand variability of small rodent diets (papers III and IV). **Fourth**, I aimed to evaluate how defences of important food items are driven by herbivory on the subarctic tundra (paper V).

Specific questions addressed in the papers were:
Paper I: Can DNA metabarcoding methods be used to study diets of small rodents?
Paper II: What do Norwegian lemmings eat during summer, and how does this vary between habitats?
Paper III: How does food selection of subarctic voles depend on food availability?
Paper IV: How does competition affect trophic niche width of arctic small rodents?
Paper V: Does herbivory induce silica-based defences of grasses in tundra habitats?

Methods

Main study area: North-East Finnmark

The Finnmark study area belongs to shrub tundra vegetation zone and is located at approximately 70°N, 27-30°E (Figures 4 and 5). Within this area, the most prominent habitat type of inland tundra landscapes (approximately 100-400 meters a.s.l., Figure 4A) is dwarf-shrub tundra heath (Figure 4A,D-E). A more productive but spatially restricted habitat is found at riparian sediment planes, where forb-rich meadows and willow (*Salix* spp.) thickets form a vegetation mosaic (Figure 4A,B-C).

In the heaths, *Empetrum nigrum* dominates the vegetation, but also *Betula nana* and *Vaccinium myrtillus* are frequent (Figure 4B-C). Field layer of the meadow vegetation is more diverse, and dominated by grasses (e.g. *Avenella flexuosa*, *Deschampsia cespitosa*), forbs (e.g. *Rumex acetosa*, *Trollius europaeus*, *Viola* spp.) and deciduous shrubs (mainly *Salix* spp.). In spite of the general common characteristics, spatial and temporal variation in vegetation composition is substantial within both habitats (Ravolainen et al. *in revision (a)*, Trasti 2010, Figure 4B-E). For example, between two consecutive years the standing crop of field layer vegetation can differ up to 50% in the meadows and 20% in the heaths (Trasti 2010).

In heath habitats, grey-sided voles are the most common small rodent species, whereas in the meadow habitats tundra voles dominate the small rodent community (Ims et al. 2011; Henden et al. 2011). In addition to voles, Norwegian lemmings are found in the area during their outbreak years. Small rodent populations in Finnmark have cyclic population dynamics with high-amplitude peaks every 4-5 years (Yoccoz and Ims 2004; Oksanen et al. 2008). During the study period of this thesis, such peaks occurred in 2007 and 2011 (see figure 3 in paper IV), with different spatial trajectories (Henden et al. 2011; Ravolainen et al. 2011, paper IV). In addition to small rodents, semi-domesticated reindeer (*Rangifer tarandus*) are abundant in the study area, whereas other mammalian herbivores are scarce (Killengreen et al. 2007).

Study designs

North-East Finnmark

Within the Finnmark study area, data was collected from three focal river catchments, namely Ifjordfjellet (IF), Vestre Jakobselv (VJ) and Komagdalen (KO) (Figure 5), using an observational study design. Two of these, VJ and KO, are at Varanger peninsula (70-71°N, 28-31°E) whereas IF is located at a mountain plateau about 100 km further west (71° N, 27° E) (Figure 5). Within each river catchment, 15 x 15 m sampling grids (KO n=24, VJ n=26, IF n=24) were established in equal numbers in the meadow and heath habitats during summer 2005 (Figure 5, hereafter called "*main study design*"). Within each sampling grid, 13 plots were established for plant biomass measurements and 8 plots for herbivore faeces counts (Figure 5). The same grids were also used for small rodent population census by snap-trapping, which provided samples for diet analyses. I used data from this study design to describe small rodent diets and assess the effects of plant biomass as well as rodent population density on them (Table 1). Additional sampling grids (n=18, 11 and 17 for IF, VJ and KO respectively) are established in heath, meadow and wetland habitats in the focal river catchments as a part of a large-scale monitoring of small rodent population dynamics (Killengreen et al. 2007; Ims et al. 2011; see description of wetland habitat in paper IV). I included small rodent samples and population density index data from these sampling grids (hereafter called "*additional trapping grids*") in papers II and IV (Table 1).

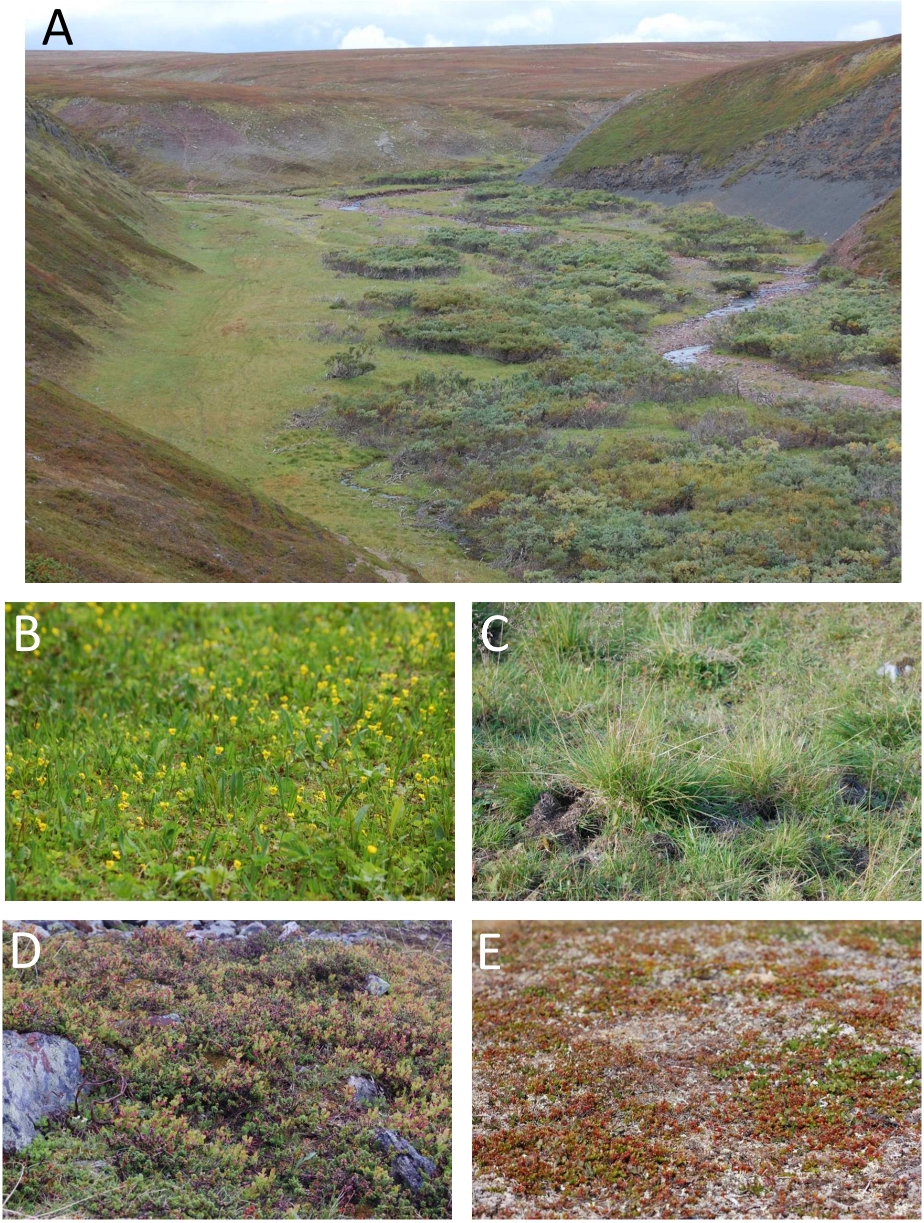


Figure 4: Landscape and examples of field layer vegetation in heath and meadow habitats of the Finnmark study area. A) Overview of a typical landscape within the study area where river valleys with willow-thickets and open meadows cut through heath plateaus, B) meadow habitat field layer, dominated by forbs C) meadow habitat field layer, dominated by silica-rich grasses, C) dense heath habitat field layer, dominated by *Vaccinium myrtillus*, D) sparse heath habitat field layer, dominated by *Empetrum nigrum*.

Within each sampling grid in the meadow habitat of the main study design, 9 experimental plots were established during summer 2006 to study herbivore effects on vegetation (Figure 5, Ravolainen et al. 2011, Ravolainen et al. *in revision (b)*, paper V). Of these, three plots were randomly assigned to each of the following treatments; (1) exclusion of rodents and reindeer using small-meshed exclosure (mesh size 1 x 1 cm), (2) exclusion of reindeer with a large-meshed exclosure (mesh size 3 x 3 cm) and (3) unexclosed control plots to which all herbivores had access. I used leaf samples of six different grasses (*Avenella flexuosa*, *Anthoxanthum nipponicum*, *Calamagrostis phragmitoides*, *Deschampsia cespitosa*, *Nardus stricta* and *Phleum alpinum*) from this field experiment to evaluate the effects of species identity, herbivore exclusion and location on grass silica content (paper V).

The three focal river catchments have coarsely similar vegetation (Ravolainen 2009, Ravolainen et al. *in revision (a)*). Since the onset of small rodent population census in 2005, rodent population densities have peaked in 2007 and 2011, but both the dominant rodent species and the temporal trajectory of the peak have differed between river catchments (Henden et al. 2011, Ravolainen et al. 2011, papers IV and V in this thesis). Moreover, the river catchments at Varanger peninsula (VJ and KO) are used as summer pastures for more than 10 000 reindeer (on average 3.2 reindeer/km^2) and thus are heavily grazed during the summer season. The river catchment IF is used by reindeer mainly during autumn and experiences thus lower grazing pressure.

Table 1: Data from the Finnmark study area included in this thesis. In each section of the table are the part of study design from which the different data were collected (uppermost, in italics) and the type of data. M, H and W refer to meadow, heath and wetland habitat, respectively.

data	river catchment	habitat	year	paper
vole traps				
rodent stomach samples	VJ, KO	M, H	2007	I
	VJ, KO	M, H, W	2007	II
	VJ, KO	M, H	2007	III
	IF, VJ, KO	M, H, W	2007-2011	IV
rodent stable isotope samples	IF, VJ, KO	M, H, W	2007-2008	IV
rodent density index	VJ, KO	M, H	2007	III
	IF, VJ, KO	M, H, W	2007-2011	IV
	IF, VJ, KO	M	2006-2008	V
vegetation plots				
plant biomass	VJ, KO	M, H	2007	III
herbivore exclosure plots				
grass silica content	IF, VJ, KO	M	2008	V
faeces plots				
reindeer density index	IF, VJ, KO	M, H	2006-2008	V

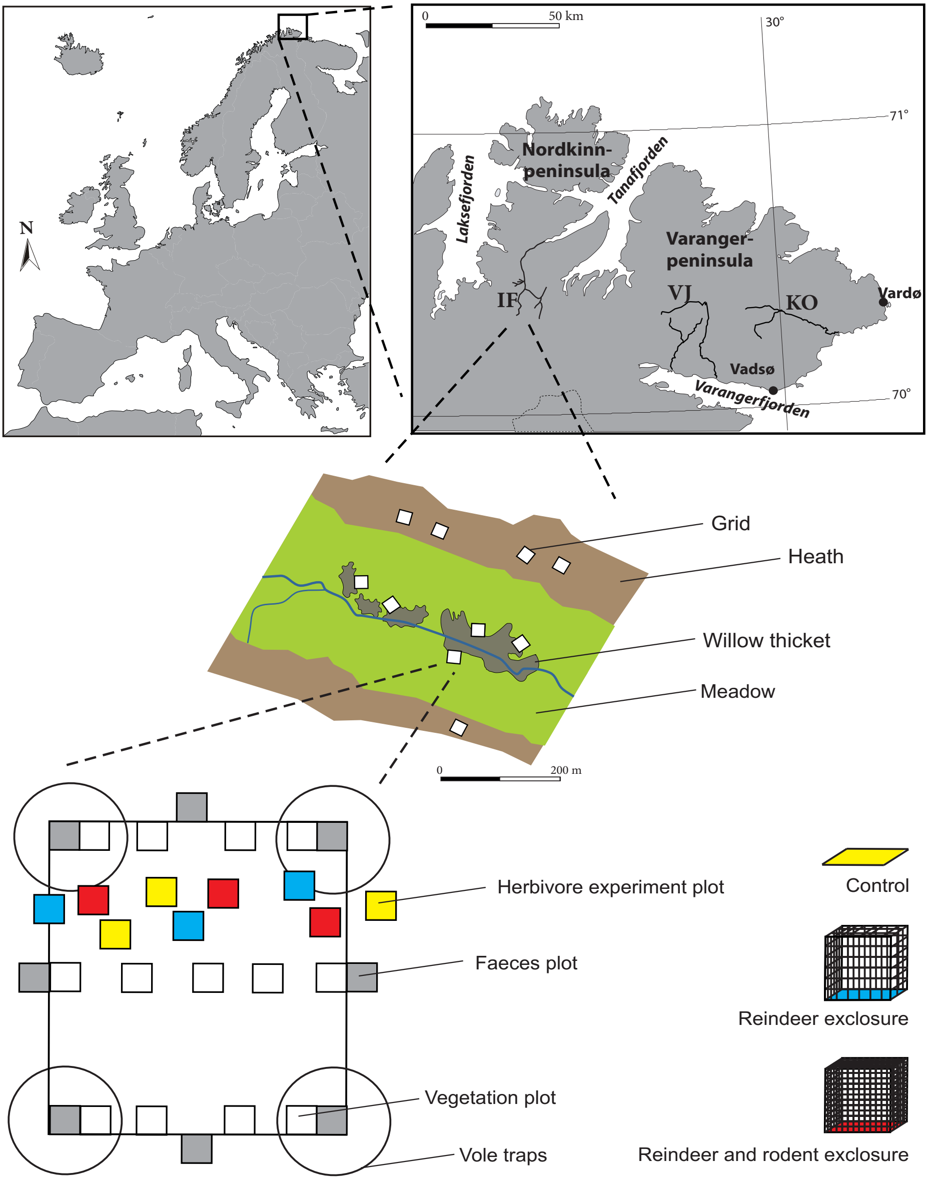


Figure 5: Main study design in Finnmark study area, which consisted of three river catchments; Ifjordfjellet (IF), Vestre Jakobselv (VJ) and Komagdalen (KO). Within each river catchment, sampling grids (15x15m, n=24 in KO and IF, n=26 in VJ) were distributed in pairs in heath and meadow habitat throughout major parts of the river catchment. Scale bar of within-catchment map is approximate, width of the river valley (i.e. the valley bottom containing willow-thicket and meadow habitat, see Figure 4A) ranged from 50m to 1.5km. Within sampling grids, study setup was identical in meadow and heath habitats except for the herbivore exclosures which were only in meadow habitat.

Other field sites (paper IV)

In paper IV, I used observational data from two additional arctic study sites, namely Nenetsky (Russia) and Bylot Island (Canada). From Nenetsky, I used stable isotope samples of tundra voles and population census data, which were collected using a study design similar to that of Finnmark, i.e. snap-trapping grids of 15 x 15 m. All of the samples were collected in riparian willow-thicket / meadow habitats, which resemble those in Finnmark (Skogstad 2009; Ehrich et al. 2012). The study site is described in more detail by Ehrich et al. (2012) and in paper IV. From Bylot Island, I used stable isotope samples of brown lemmings (*Lemmus trimucronatus*), collected by snap trapping from two dominant habitats of the study site; wet and mesic tundra. I also used population density data, achieved by mark-recapture methods, and described in detail in (Gruyer et al. 2008). Further details on the small rodent trapping on Bylot Island, as well as description of the study site are given in paper IV and in Gauthier et al. (2011)

Greenhouse experiment (paper V)

In paper V, I combined two experimental designs to study silica induction of grasses; herbivore exclosure plots from the field (Table 1) and an additional experiment in a greenhouse. The greenhouse experiment, designed to identify genotypic variation on grass silica induction, encompassed four common subarctic grass species (*Avenella flexuosa*, *Anthoxanthum nipponicum*, *Deschampsia cespitosa* and *Festuca ovina*). I tested the effects of simulated grazing, genotype identity and their interaction on foliar silica levels of each species using a factorial experimental design.

Small rodent diets

Microhistology

I used three different methods to study diets. First, I tested the traditionally used microhistological methodology, which is based on identifying plant epidermal fragments of stomach contents, or faeces, of a herbivore (Hansson 1970; Johnson et al. 1983; Carrière 2002). Taxon identification using this method requires a reference collection of microscopy photos of plant epiderm, covering flora of the focal region. With systematic counting of identifiable fragments and comparison with reference collection, one can then achieve a quantitative estimate of stomach contents. In paper I, I used this method as a reference to the application of novel DNA metabarcoding methods on small rodent diet studies.

During summer 2006, a sample of each vascular plant species present at the sampling grids at Komagdalen and Vestre Jakobselv was collected and dried. I used these samples to construct a reference database of microphotographs of each species leaf epiderm, as well as stems, seeds, root and fruits of certain species of special interest. Using a method modified from (Hansson 1970) I prepared the stomach contents to analysis by first homogenizing the content and then filtering it to $>$ 0.16 mm and $>$ 0.56 mm fractions. I then bleached the samples with approximately 2 ml of household bleach for approximately 1/2 hour, and analysed one microscope mount from each fraction. From each mount, I counted 25 hits on identifiable material along a measuring grid, under a light microscope (40x).

DNA metabarcoding

The second type of methodology I used for studying small rodent diets was DNA metabarcoding, i.e. taxon identification using a standardized genome section (Valentini et al. 2009b; Taberlet et al. 2012). For the diet studies of herbivorous small rodents it was important to use a method which would identify a large range of plant taxa as detailed as possible. Therefore, I had three important criteria for selecting the targeted DNA region. First, in order to distinguish between taxa, the selected region had to differ between taxa. Second, stomach content samples contain mostly degraded DNA, i.e. the DNA molecules are not of original length but have been broken to short fragments. It was therefore also important that the targeted region was short. Third, DNA just outside the targeted variable region had to be very similar amongst taxa. In order to multiply DNA using polymerase chain reaction (PCR), two so called primers are required. Primers are short DNA-fragments which attach to the sample DNA, multiplying the DNA section between them during PCR (See example in Figure 6A). Therefore, to achieve amplification of the targeted DNA in all targeted taxa, primer attachment sites have to be similar amongst them. So called ”universal primers”, i.e. primer pairs which amplify a short and variable DNA region across a large range of taxa have been developed for plants and fungi (Taberlet et al. 2007; Epp et al. 2012). For seed plants (i.e. spermatophytes) I used the so-called *g-h* primer pair (Taberlet et al. 2007) and for fungi the primer pair *ITS-Fungi* (Epp et al. 2012) (Table 2).

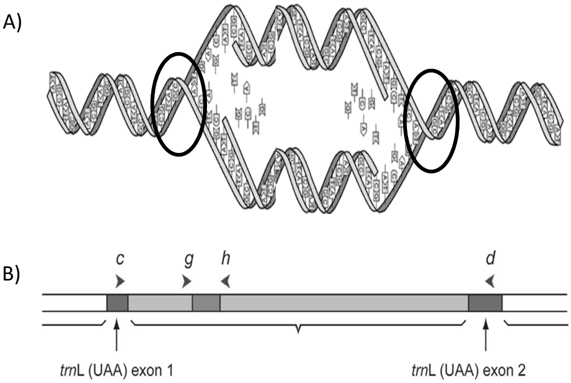
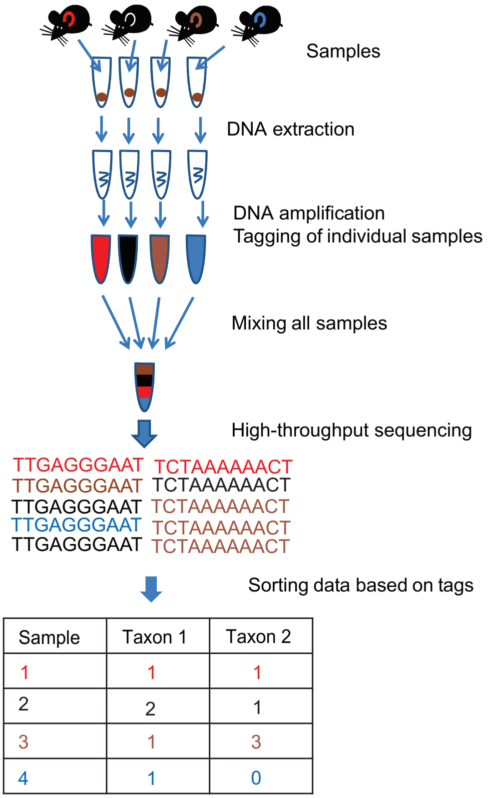


Figure 6: A) schematic illustration of a DNA fragment with primer attachment sites. B) primer pairs *g-h* and *c-h*. Figure adapted from Taberlet et al. (2007)

In addition to seed plants, I expected to find mosses in lemming diets. I therefore wanted to both evaluate the proportions of mosses, seed plants and other vascular plants in lemming diets, as well as identify the most important moss groups. To achieve this, I used primers *c* and *h* (Table 2, Taberlet et al. 1990, 2007). Primer pair *c-h* includes same region as primer pair *g-h*, together with an additional region (Figure 6B). It thus enabled separation of mosses and vascular plants as well as identification of moss groups. It also amplified short enough DNA-region to be used on stomach content samples.

Table 2: DNA metabarcoding primer pairs used in this thesis.

taxon	primer name	targeted DNA region	paper	reference
seed plants	*g-h*	chloroplast *trn*L (UAA) intron	I-IV	Taberlet et al. (2007)
all plants	*c-h*	chloroplast *trn*L (UAA) intron	II	Taberlet et al. (1991, 2007)
fungi	*ITS-Fungi*	ITS1 -region of nuclear DNA	II	Epp et al. (2012)



Sample	Taxon 1	Taxon 2
1	1	1
2	2	1
3	1	3
4	1	0

Figure 7: Principle of the workflow of DNA metabarcoding.

In practice, DNA metabarcoding data is achieved as follows. First, all DNA present in a sample (e.g. a stomach content of a rodent) is extracted (Figure 7). Thereafter, targeted DNA fragment is amplified using PCR. This results in a sample with a large number of copies of the targeted DNA-region, but a minute number of non-target DNA copies. After amplification, the DNA is purified and quantified, i.e. the concentration of DNA per sample is analysed. The individual samples are then mixed, taking their concentrations of DNA into account, to achieve a pooled sample into which each individual sample has contributed with as much DNA (Figure 7). In order to identify individual samples from this pooled sample later on, the samples have to be tagged. This routinely happens by adding a tag sequence on the primer sequence before the PCR (Coissac et al. 2012). The pooled sample is thereafter sequenced using a high-throughput sequencer, resulting in a dataset where all sequences from all individuals are mixed (Figure 7).

After the sequencing, bioinformatic tools are used to first remove erroneous sequences from the dataset and thereafter to identify the original individual samples as well as taxa they contain (Figure 7, Coissac et al. 2012). To include only reliable DNA sequence data, all metabarcoding data in this thesis (papers I-IV) was cleaned using OBITools -software package (http://www.prabi.grenoble.fr/trac/OBITools). Here, I describe the principle of the cleaning, while details are given in the respective papers. First, sequences with errors in primer and tag sequences were excluded. Thereafter, very rare sequences were excluded. Two additional steps were added in the cleaning of data for papers II and IV. Sequences which occurred in an intermediate form; i.e. had apparently mutated from their original form during PCR were excluded using a clustering algorithm (Shehzad et al. 2012). Also, sequences which were of unrealisticly short length were removed.

The cleaned dataset was then compared to reference libraries containing known sequences. For primer pair *g-h*, I used a reference library of 842 arctic vascular plant species (Sønstebø et al. 2010). In papers I and III, sequences which matched poorly with these references were further compared with target sequences extracted from a public reference library, GenBank (http://www.ncbi.nlm.nih.gov/genbank/). In papers II and IV, I supplied the arctic reference library with 877 boreal vascular plant taxa at the rank of species, subspecies or variety (Brochmann et al. unpublished). In these papers, I further compared the poorly matching sequences against those that are publicly available in the EMBL Nucleotide Sequence Database (http://www.embl.de/index.php). Even if EMBL and GenBank are hosted by different institutions, they frequently exchange sequences and thus contain the same data. For primer pair *c-h*, I further supplied the reference library of arctic and boreal vascular plants with sequences of 442 arctic and boreal bryophyte species (Gussarova et al. unpublished) to identify moss taxa. No targeted reference library was available for *ITS-Fungi* and I therefore used only sequences retained from EMBL. A final step of sequence data cleaning was done at this stage, excluding sequences which matched poorly with any known taxa.

The final clean dataset always consisted of a count of different taxa per individual. However, the actual number of sequences per individual has little biological meaning. I therefore used two different approaches to include all individuals in a common analysis. For all data on plants (Table 2), I transformed the counts to proportions within an individuals diet. Due to the potential biases of DNA metabarcoding data (paper I, Pompanon 2012), I also calculated frequency of occurrence of plant taxa within a rodent species diet (papers II and III). For the data on fungi (primer pair *ITS-Fungi*, paper II), I only report the frequency of occurrence, as no evaluation of the quantitative aspects exists for this primer pair.

Stable isotopes

In paper IV, I used a third method to study small rodent diets, namely stable isotopes. This method is based on ratios of different isotopes within carbon (δ^{13}C) and nitrogen (δ^{15}N), which in a consumers tissue reflect those of its food sources. As tissue build-up takes long time in comparison to filling up a stomach, stable isotope ratios of tissues incorporate a consumers diet across longer time-periods than what can be measured using stomach content analysis. Thus, stable isotope studies are used in increasing amounts to illustrate many aspects of feeding ecology which are difficult to study using more conventional methods (see a recent review by Ben-David & Flaherty 2012).

I used stable isotope ratios to compare diets of groups of individuals against each other. This approach is based on so called ”isotopic niche”, i.e. the niche occupied by a group of individuals in isotopic space (Newsome et al. 2007). Isotopic space can be, in its most simple form, represented as a bivariate plot; δ^{13}C and δ^{15}N along the two axes. The relative sizes and positions of such isotopic niches can then be used to infer differences in feeding ecology between the compared groups. A detailed description on the samples, laboratory analyses and data analyses is included in paper IV.

Grass silica content; plant defence data

Foliar silica content of samples from both the field and greenhouse experiment was analysed using X-Ray Spectrometry. Leaf samples were first dried and grinded, then pressed into 13 mm pellets using a hydraulic press at 11 bars. The pellets were subsequently analysed using a Niton XL3t portable XRF analyzer (Thermo Fisher Scientific, Inc.), calibrated against silicon-spiked synthetic methyl cellulose.

Focal predictor variables

Population density indices for herbivores

An index of small rodent population density in the Finnmark study area was collected using small quadrate snap-trapping method according to Myllymäki et al. (1971). The trapping was done twice each year, once in early/mid-July and once in early September. More details of the trapping are published by Henden et al. (2011) for the main study design and by Ims et al. (2011) for the additional trapping grids. In paper IV, I also used similar snap-trapping data from the Nenetsky study area and population density estimates based on live-trapping from Bylot Island (details presented in paper IV).

An index of reindeer density for the main study design of Finnmark study area was gained by faeces counts. These counts were conducted annually in early July and early September. During each count, presence of reindeer faeces was recorded in 8 permanent plots (50 x 50 cm) per grid (Figure 5), and the plots were subsequently cleaned of faeces. Thus, July counts represent reindeer presence during the preceding winter, and September counts during the preceding summer.

Plant biomass; food availability data

Plant biomass data was collected during the peak of growing season (late July/ early August) using point intercept method (Jonasson 1988; Bråthen and Hagberg 2004). In each sampling grid of the main study design, these measurements were done in 13 sampling plots of 50 x 50 cm (Figure 5, see Table 1 for grids included in this thesis). In each plot, number of hits on 20 pins was recorded and subsequently converted to biomass estimates using calibrations presented by Ravolainen et al. (2010). Hits were recorded at plant species level, thus enabling the aggregation of data to different food item units, such as plant families or functional groups.

Results and discussion

Methodology to study herbivore diets (based on papers I, II and IV)

DNA metabarcoding and microhistology

Comparison between DNA metabarcoding and microhistology revealed that DNA metabarcoding was taxonomically much more detailed, more objective and less biased between taxonomic groups (paper I). Both methods agreed on the general picture of the diets of the two vole species included in the study, i.e. similar conclusions could be drawn about the importance of most food item groups for a vole species. Some plant groups did, however, behave differently in the different analysis. While these discrepancies were primarily due to different taxonomic resolution, microhistology is biased towards easily identifiable groups (paper I, Alipayo 1992). On the other hand, food item proportions gained by DNA metabarcoding are potentially also biased, and such results should be presented together with frequencies of occurrence of food items (Deagle et al. 2006; Pompanon et al. 2012). Main biases of this method are due to different number of DNA copies in different plant tissues, as well as different length of DNA fragments leading to preferential amplification of short fragments (Pompanon et al. 2012). Even so, the general agreement of proportions between methods indicates that such issues do not severely hamper the use of DNA metabarcoding for herbivore diets (paper I). A conclusive evaluation of the accuracy of proportional DNA metabarcoding data would still require controlled feeding experiments where ingested food proportions could be related to those observed in diets.

Both methods require a great amount of training, but the equipment needed for metabarcoding is more specialised than that required by microhistology. Still, most studies using microhistology to investigate small rodent diets have been done during 1960-1980's (see references within "Introduction: Diets of tundra-dwelling small rodents"), after which little new knowledge of small rodent diets has been gained. Later research on small rodent feeding habits has mostly focused on experiments where impacts of rodents on vegetation has been measured (Strengbom et al. 2003; Dahlgren et al. 2007, 2009), although some exceptions exist (Saetnan et al. 2009). Such a lack of newer studies seems to indicate that the knowledge of small rodent diets which could be gained with further microhistology studies is not likely to add greatly to the current understanding. Thus, to address further questions on the characteristics of small rodent diets, their variability and how that relates to different ecological variables, different methods are needed. While I used stomach contents in the papers included in this thesis (papers I-IV), non-lethal diet studies would be preferable. DNA metabarcoding of faeces makes this possible (Box 2), and while population-level data could be gained by collecting faeces from the wild, individual-level data would require a more specific study design based for instance on live-trapping.

Microhistology could still reveal some aspects of small rodent diets that DNA metabarcoding could not. For example, separating different plant tissues is only possible by visual examination of stomach contents. Thus, microhistology could be used to determine the proportions of plant parts such as leaves, seed, berries or woody tissue in small rodents diets (Hansson 1970). Such knowledge could open avenues for more detailed studies of small rodent diets, if used in combination with a taxonomic approach and DNA metabarcoding.

What can different primer pairs, alone and together, tell?

In papers I, III and IV, I only used primer pair *g-h*. This primer pair targets a short sequences of chloroplast DNA, which base-pair composition differs sufficiently between spermatophyte (i.e. seed-plant) species to enable their identification. Thus, it provides a useful approach for studying seed plants, but the complete picture of diets of herbivores which consume great amounts of other plant taxa, such as mosses and horsetails, cannot be gained with this primer pair alone. Also, some spermatophyte families, mainly Asteraceae, Salicaceae and Poaceae, can rarely be identified to species level using this primer pair. Again, depending on the question this can be problematic or not. For example *Salix* spp. thickets in Finnmark are composed of a great number of species, whereas only *Salix herbaceae* is common in the heath habitat. Thus, identifying family Salicaceae in herbivore diets at the meadow habitat may refer to many different species, whereas in the heath habitat a more precise identity can be inferred based on the vegetation.

In paper II, I supplied the *g-h* primer pair with *c-h* and *ITS-Fungi* (Taberlet et al. 1991, 2007; Epp et al. 2012). The *c-h* primer targets a longer area than *g-h*, which enables identification of also mosses. For lemmings, which are feeding on mosses in addition to seed plants (paper II and references therein), such additional analysis was necessary to properly evaluate their diet. The combined approach enabled estimation of moss and vascular plant proportions in lemming diet, as well as more details on which taxa within these groups were consumed.

For both *g-h* and *c-h* primer pairs I was able to compare the sequence data against a reference library of target sequences from arctic flora. For fungi, such reference library does not exist currently and sequences extracted from an open database (EMBL, http://www.ebi.ac.uk/embl/) had to be used. Publicly available sequences are not always of good quality and some of them may be misidentified. Thus, any accurate results of herbivore diets require a targeted database covering the focal regions flora. I could further improve the accuracy of taxon identification by comparing the identified taxa to those present in the study area, i.e. the potential species pool (papers I-III). Especially in areas with low number of species within family, such as the arctic, data on focal flora can greatly improve the resolution of DNA metabarcoding data.

Stable isotope ratios and small rodent diets

In paper IV, I used stable isotope ratios to complement DNA metabarcoding analyses on small rodent diets. Interestingly, I found no differences in small rodents isotopic niche between habitats, even though DNA metabarcoding data showed clear indication of differing diets between habitats (paper IV). The stable isotope ratios of any tissue reflect those of a consumers diet during the buildup of that tissue (Ben-David and Flaherty 2012). Muscle tissue, which I used, has a build up time in other rodents for about a month (Miller et al. 2008), although no measurements for my study species exist. It seems likely that the time-window of isotopic niche based on muscle is too long to capture differences in diets between habitats. Small rodents have small and usually stable home ranges (Rodgers and Lewis 1986; Erlinge et al. 1990), and could therefore be expected to forage nearby the location they were trapped. However, it seems that rodents trapped outside their primary habitat may not necessarily have spent their whole life there but have migrated from elsewhere. The time-frame of one month can be relatively long in regard of the lifespan of a small rodent as well as the processes which can be expected to have an impact on small rodent diets. Tissues with faster build-up rate than muscles, such as blood, could potentially better elucidate processes at a time-scale relevant for small rodents food selection within a home range.

Moreover, herbivorous small rodents have available a wide range of food plant taxa even in the high arctic (see e.g. the Panarctic Flora, available at http://nhm2.uio.no/paf/). Even though the isotopic ratios of these plants do vary between species, not all taxa differ distinctly from each other (paper IV). It is therefore relatively challenging to interpret isotopic ratios as real food proportions, which is possible for distinct food sources using so called mixing models (Phillips 2012). This is a common approach in predator diet studies (Ben-David and Flaherty 2012), but probably useful for herbivore diet studies only when food plants can be grouped into for example marine vs. terrestric or C4-plants vs. C3-plants (Chambers and Doucett 2008; Inger et al. 2006; Ben-David and Flaherty 2012). However, an interesting possibility to assess the contribution of fungi to herbivores diets may lay within the use of mixing models, as the stable isotope ratios of plants and fungi differ more distinctively than those among plants (Trudell et al. 2004). Still, mixing models require several estimates of consumer species physiological processes (Ben-David and Flaherty 2012), for which data is currently lacking for many herbivores.

In spite of these limitations, variation of stable isotope ratios between groups of individuals can give valuable information on herbivore feeding habits at population level, given that the variability present in the underlying food items is appropriately evaluated. For example, in paper IV I show that stable isotope ratios of plants in tundra habitats were above all defined by plant species identity. Thus, I could conclude that an increase of a small rodent populations isotopic niche width with population density was likely caused by an increased range of consumed plant species.

New insights on small rodent diets in Finnmark (papers I-IV)

For all the three small rodent species which diets I studied in detail, the DNA analyses gave partly surprising results. On one hand, I identified a greater number of plant species in the diets of all three rodent species (grey-sided vole *Myodes rufocanus*, tundra vole *Microtus oeconomus* and Norwegian lemming *Lemmus lemmus*) than what has been recorded before (papers II and III). On the other hand, within the plant groups that most previous diet studies have identified, some species were clearly eaten more than others (papers II and III). The wide range of commonly consumed taxa indicates that at least the two vole species can be considered as generalist herbivores (as defined in Box 1). The diet of Norwegian lemming was, however, dominated by a few food items, implying that lemmings have a somewhat more specialised diet than voles. Still, as lemming diets include various other taxa in addition to the dominant ones and they forage across a wider range of taxa than that of voles (i.e. including both vascular plants and mosses), I suggest that the description generalist herbivore is also appropriate for lemmings.

My results also indicate that fungi seem not to be actively eaten by lemmings and voles (paper II, Box 3). Although almost all investigated individuals of all three rodent species had ingested some fungal taxa, those fungal taxa that could be identified belonged mainly to micromycetes, i.e. to taxa which produce no large fruit bodies that could be used as food. Rather, many identified taxa have such ecology that they probably have been eaten together with the plants foods, being for example plant pathogens, endophytes, or root associated fungi. Plant-associated fungi in tundra habitats are diverse (Newsham et al. 2009; Jensen et al. 2011), although little is known about their ecology. In other ecosystems, such fungi have been found to sometimes have implications for herbivores through modified food quality (Saikkonen et al. 2006; Huitu et al. 2008; Saari et al. 2010). Thus, the indirect role of fungi for rodents remains an intriguing question.

Myodes rufocanus

Grey-sided voles diets in tundra heath habitats were dominated by ericoid shrubs and forbs (papers I and III). However, their diets were clearly more diverse than previously

Box 2: Is it necessary to kill rodents to know what they eat?

In this thesis, I have used stomach contents of small rodents to study their diets. Because the population censuses in the Finnmark study area were done with snap-trapping, dead animals were available to be used for additional research purposes. However, in many cases it would be more appropriate to use non-lethal methods of diet analyses. In paper I, I suggest that collecting faeces would be a good alternative for stomach content studies.

When food is passed through a digestive system, DNA of different food items may be degraded to a different degree. To evaluate the use of faeces instead of stomach contents, I compared the two approaches. I collected both stomach contents and pellets from the rectum in a total of 40 individuals. Both stomach contents and pellet contents were then analysed using DNA metabarcoding methods as described in paper I. I then compared the species-specific diets based on data from pellets and stomach contents (Figure **B2-1.**).

Assessed at population level, diets reflected by stomach contents and pellet contents are rather similar. Moreover, DNA metabarcoding methods have been successfully used to assess diets from faeces of various other herbivores (Valentini et al. 2009a; Kowalczyk et al. 2011; Raye et al. 2011; Ait Baamrane et al. 2012). These results indicate that sampling pellets could be a good alternative for stomach content analysis and lethal methods on future small rodent diet studies could be avoided. While faeces sampling from traps during live-trapping could provide similar resolution of species and individual as stomach content studies, faeces sampled from the field are both difficult to identify to rodent species and potentially contaminated by surrounding plant DNA. Such a loss of resolution could be tackled with a careful sampling design and additional DNA analyses to identify the rodent species in question.

In combination to non-lethal DNA metabarcoding diet studies, also non-lethal stable isotope methods are an option. Several tissues can be sampled from live-trapped animals, such as fur, whiskers and blood. A combination of quickly renewed tissues, such as blood, and slowly renewed tissues, such as fur, could give insight to changes in an individuals diet through its life. Such an approach has been suggested by Bearhop et al. (2004), but to my knowledge never attempted on herbivores.

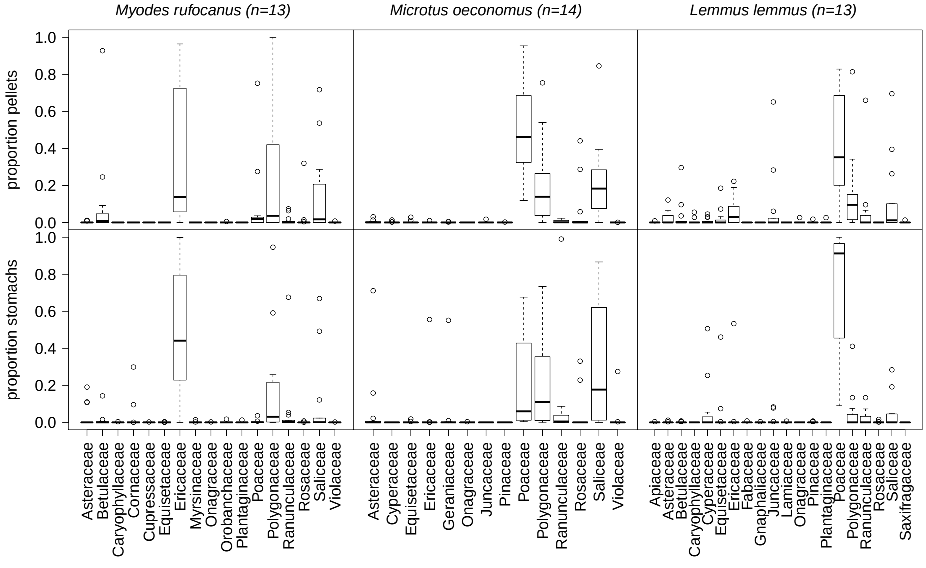


Figure B2-1. Proportions of vascular plants in stomach and rectum of digestive system of three small rodents species. Data from the same individuals are included in both upper and lower panels.

considered (paper III). Surprisingly, grey-sided voles seem to include various ericoids shrubs in their diets; in addition to *Vaccinium myrtillus* I found *V. uliginosum* and *Empetrum nigrum* to be rather common, and a range of other ericoid species also present. Local food availability seems to have a clear effect on the grey-sided voles diet, as individuals trapped during summer season and in meadow habitats ate more forbs and grasses but less ericoid shrubs, than those from heath habitats and during autumn season (papers III and IV).

Microtus oeconomus

In the tundra meadow habitats, tundra vole stomach content were dominated by forbs, which they also selected for (papers I and III). My results thus contradict clearly the earlier characterization of tundra voles as a graminoid-feeding species (Tast 1974; Batzli and Jung 1980; Batzli and Henttonen 1990). As discussed in paper III, this is probably due to a combination of methodology and availability. Moreover, I found that animals captured from heath habitats had consumed more than average proportion of ericoid shrubs and grasses (paper IV), both groups typically more abundant in heaths than forbs. Thus, also tundra vole diets are clearly modified by local food availability.

Lemmus lemmus

I found the diets of Norwegian lemmings to be dominated by mosses and graminoids (paper II), which is in agreement with previous studies (Kalela et al. 1961; Koshkina 1961; Stoddart 1967; Hansson 1969; Tast 1991; Saetnan and Batzli 2009). However, the DNA metabarcoding methodology made it possible to identify some of the dominant taxa, namely *Avenella flexuosa* within grasses and *Dicranum* sp. within mosses (paper II). Even if I found in total 27 vascular plant genera, the diets of lemmings were rather dominated by the above-mentioned taxa and thus clearly less diverse than vole diets (papers II and IV). Lemmings, too, seem to show some variation in diets between habitats, although a more balanced sample size would be needed to confirm the trends I found (papers II and IV).

Why do small rodents eat what they eat (papers III and IV)

In papers III and IV, I evaluated the effects of food availability and competition on small rodent feeding habits. In summary, I found that voles preferred nutritious and easily digestible functional groups (and taxa within them) more than less palatable taxa (paper III, Box 5). Seasonal changes in vole feeding habits (paper III), responses to available biomass (paper III) as well as differences in diets between habitats (paper IV), indicate that changing food availability and quality modify these preferences. While seasonal changes in diets can be caused by a combination of decreased nutritional quality and biomass of herbaceous foods towards the autumn, variability of diets between habitats is probably caused by the habitat-specific biomass of different food items. Availability of alternative food items has an impact on vole selectivity, to the extent that the biomass of food items which are less preferred at the rodent population level, may modify the consumption of more preferred food items (paper III). Thus, these results indicate that even if food quality probably is important in determining rodents absolute preferences, the relative availabilities of food items seem to be important determinants of the realized preferences.

Further, I found little indication that small rodents would compensate low availability of some foods by increased selectivity (paper III). Increased availability of a food item tended rather to increase selectivity for it (paper III). My interpretation

Box 3. Fungi in vole diets?

Little is known about the presence of fungi in vole diets, what type of fungi are ingested and whether they have any physiological or ecological implications for voles. While fungi are only seasonally available as food (mushrooms in the autumn), voles may also ingest fungi with their plant foods. I analysed stomach content of grey-sided voles (n=86) and tundra voles (n=62) for fungi, following methods described in paper II. Most vole individuals had ingested fungi; only 8% of grey-sided voles and 11% of tundra voles contained no fungi at all (Table B3-1). However, based on those fungi which could be identified to species or genera, macromycetes do not seem to be commonly ingested food items (Table B3-1). The only identified macromycete taxa was *Russula* sp., which was found in 10% grey-sided voles. Interestingly, one of the identified taxa (*Claviceps purpurea*) is know to be an endophytic fungi which produces compounds that are toxic for herbivores (Lev-Yadun and Halpern 2007).

Table B3-1. Frequency of occurrence of fungi in diets of tundra voles (”Mo”) and grey-sided voles (”Mr”) Column ”size” refers to micromycetes (”mi”) and macromycetes (”ma”). Taxa marked ”NR” refer to taxa with ”no rank”, i.e. taxa which position within larger taxa is unclear.

division	Family	Species	Mo	Mr	Size
Ascom			45	43	
	Venturiaceae		11	5	
		Venturia sp.		2	mi
		Venturia atriseda	11	2	mi
	Davidellaceae	*Cladosporium cladosporioides*	2		
	Leptosphaeriaceae	*Leptosphaeria* sp.	9	1	
	Mycosphaerellaceae	*Mycospharella* sp.		5	
	Sporormiaceae	*Preussia* sp.		1	
	Pleosporales NR	*Ochrocladosporium elatum*		1	
	Helotiaceae	*Gremminella* sp.	2	5	mi
	Helotiales NR			2	
		Phialocephala cf. *fortinii* GS15P1c		1	
	Thelebolaceae		2	3	
	Trichocomaceae	*Penicillinium* sp.		2	
		Penicillium dipodomyicola		2	
	Dipodascaceae		6	14	
		Galactomyces geotrichum		6	mi
		Yarrowia lipolytica	6	10	mi
	Clavicipitaceae	*Claviceps purpurea*	2	1	
	Halosphaeriaceae	*Monodictys arctica*	5		
	Hyponectriaceae	*Pseudomassaria chondrospora*		1	
	Hypocreales NR			1	
	Xylariales NR	*Microdochium* sp. 5/97-37	10	1	
	NR	*Troposporella* sp.		2	
Basidiom			41	37	
	Exobasidiaceae	*Exobasidium rostrupii*	5	5	mi
	Schizophyllaceae	*Schizophyllum* sp.	3	14	ma
	Amanitaceae			4	
		Amanita sp.		3	
		Amanita vaginata		1	
	Russulaceae			10	
		Russula sp.		10	
		Lactarius tabidus		1	
	Tremellales NR		10	8	
		Dioszegia crocea	6	1	
		Bullera sp.	2		
	Leucosporidiales NR	*Leucosporidium* sp.		2	mi
Chytridiom	Rhizophydiales NR			2	
NR			87	84	
	Mortierellaceae	*Morteriella* sp.	2		
	Mucoraceae			6	
		Mucor racemosus		2	
	No rank fungi	fungal endophyte sp. M4-3261	2		
		fungal sp. SUN1	1		

of this result is that when food item availability is low, small rodents do not invest extra time in finding these food items. In paper III, I discuss the potential reasons for this, and suggest that predation risk avoidance could greatly affect the time use by rodents.

Moreover, I found that when small rodent population density increases, their population-level dietary diversity tends to increase (paper IV). Density had, however, no impact on the diet composition at the population level, implying that the increased diversity of diet was caused by different responses of different individuals. This indicates that at higher population densities, the inclusion of new food items in diets depends on availability, different individuals including different food items. On the other hand, increased population densities tend to lead to a spillover of individuals to habitats adjacent to their primary habitat (Henttonen et al. 1977; Oksanen et al. 1999; Morris et al. 2000; Sundell et al. 2012; paper IV). Because individual diets are affected by the habitat-specific availability of different food items, such increased habitat use heterogeneity tends to increase the population diet diversity (paper IV). Together, these results indicate that both bottom-up (food availability) and top-down (predation risk) interactions in a food web, as well as competitive interactions, play an important role for small rodent food selection in the wild.

Based on these results, I suggest that small rodents food selection, and that of herbivores in general, should be seen as a hierarchical process, where constraints of time and habitat use may partly overshadow the nutritional effects. Thus, for example predation risk avoidance may constrain both habitat selection and time available for foraging (as indicated by Nersesian et al 2012a), consequently resulting in less selective, broader diets which reflect more closely food availability than diets in the absence of such a constrain. Hierarchical processes of herbivore feeding behaviour have been studied in large herbivores, but with a focus on resource availability at different spatial scales (Senft et al. 1987; Bailey et al. 1996). While a conceptual framework of relevant spatial scales for large herbivore foraging decisions has consequently emerged (Senft et al. 1987; WallisDeVries et al. 1999; Bailey et al. 1996; Searle et al. 2008), similar understanding of small herbivores decision scales is currently lacking. Further, the importance of different ecological interactions on foraging decisions at different spatial scales is little acknowledged (Searle et al. 2008), and warrants further research.

Role of grass silica defences in tundra food webs (paper V)

In the greenhouse experiment, I found that at least part of the common grasses of tundra habitats have the capacity to induce silica as a response to herbivory. However, this ability clearly differed between genotypes of the same species. Moreover, I found no clear increase of silica levels due to herbivory in the field, but variable silica levels in different locations. I discuss potential explanations for these findings in paper V, and suggest that spatially variable growing conditions and adaptations to herbivory caused the lack of a uniform response.

Previous research on interactions between voles and grass silica defences has mostly been conducted in conditions where grasses have been the main available food source for voles (Massey and Hartley 2006; Massey et al. 2007, 2008). In Finnmark, silica-rich grasses as well as grasses in general form a small proportion of vole and lemming diets (Box 5, papers II and III). As these small rodents also have plentiful other food sources available (paper III) they probably switch to feed on alternative food items if silica content of grasses increases to unpalatable levels. Silica-based defences of grasses are thus likely to have an indirect impact on small rodent diet quality, rather than directly impacting small rodent health with consequent effects on their population dynamics. Hence, the lack of a clear and uniform response of grass silica levels on

Box 4: Potential for exploitation competition between small rodent species?

During cyclic population density peaks, several small rodent species are found in habitats adjacent to their primary habitat, and their habitat use thus overlaps with other small rodent species (Henttonen et al. 1977; Oksanen et al. 1999). Interaction between species under such conditions has been little studied, although some indication of interference competition exists (Henttonen et al. 1977). However, two species present in the same habitat may also experience exploitation competition if a) their diets overlap and b) resources are limited.

To evaluate the potential for interspecific exploitation competition between small rodents in the subarctic tundra habitats of Finnmark, I measured overlap between their diets. I included all stomach samples presented in papers I-IV, analysed for vascular plant content at plant family level (*Lemmus lemmus*, n=55, *Microtus oeconomus* n=111, and *Myodes rufocanus* n=154). Details of methods are given in papers I (laboratory) and IV (field and bioinformatics). To measure overlap, I used Schoeners index of diet overlap (Schoener 1968), which takes values between 1 and 0, 1 indicating complete diet overlap and 0 no diet overlap.

Table B4-1. Diet overlap between small rodents from Finnmark, measured as Schoeners index. Above to right are results from heath habitat (*L. lemmus*, n=36, *M. oeconomus* n=21, and *M. rufocanus* n=117), below to left from meadow habitat (*L. lemmus*, n=12, *M. oeconomus* n=90, and *M. rufocanus* n=37).

	L. *lemmus*	*M. oeconomus*	*M. rufocanus*
L. lemmus	-	0.45	0.29
M. oeconomus	0.43	-	0.74
M. rufocanus	0.49	0.69	-

Based on Table B4-1, overlap between vole species seems to be higher than that of between lemming and voles. These results probably underestimate the difference as the index values are based on vascular plants only and the high proportion of mosses in lemming diets (paper II) has not been taken into account. As these results are based on plant family level, some biases may occur. For example, within Poaceae lemmings feed mainly on the grass *Avenella flexuosa* (paper II), whereas both vole species include a more varied range of grass species in their diets (papers I and III, Box 5). Nevertheless, these results indicate potential for exploitation competition, especially between vole species, when they occur together.

herbivory (paper V) is probably also related to the availability of alternative good quality food items. Accordingly, availability of alternative good quality food items is likely to be an important factor shaping the interaction between small rodents and grasses, not only in Finnmark but also in other ecosystems.

Still, silica-based defences of grasses do seem to have a further role in plant-herbivore interactions in tundra habitats. Even if grasses did not seem to respond to herbivory by inducing silica, biomass of silica-rich species decreased with reindeer exclusion in the same exclosure experiment (Ravolainen et al. 2011). It thus seems that heavy reindeer grazing may maintain the presence of silica-rich grasses in vegetation, similarly to that of sheep grazing (Austerheim et al. 2007). While reindeer grazing directly reduces the biomass of preferred palatable plants (Bråthen and Oksanen 2001), it probably also provides competitive advantage for silica-rich grasses as indicated by (Ravolainen et al. 2011). Such an advantage can either be caused by lower grazing pressure due to lower palatability for herbivores, better grazing tolerance, or a combination of these. Moreover, it is likely that high silica content improves the competitive ability of grasses, through increased rigidity and stress tolerance (Currie and Perry 2007; Cooke and Leishman 2011). Furthermore, two of the most common silica-rich grasses of Fennoscandian tundra habitats, *Deschampsia cespitosa* and *Nardus stricta*, form dense tussocks. Such tussocks show frequently signs of rodent grazing, even though these grass species are not important for rodents as food (Box 5, papers II and III). Rather than food, silica-rich tussock grasses are likely to function as a shelter from especially avian predators in the otherwise open tundra landscape. Consequently, the role of silica-rich grasses for small rodents in tundra habitats seems to be partly in creating sheltered habitat and partly in outcompeting more palatable food plants, such as forbs. Hence, silica rich grasses probably form an interaction link between small rodents and reindeer in tundra habitats.

Box 5: Do voles feed on silica-rich grasses?

To understand the role of silica-rich grasses in tundra ecosystems, one obvious question is: do herbivores feed on them? During vole population peaks, especially *Deschampsia cespitosa* tussocks on tundra meadows are full of tunnels (see e.g. Figure 4C, photo in the front cover of paper III). Living plants area clearly cut by voles, and grass litter is abundant. However, grasses are not very abundant in tundra vole diets and tundra voles feed on monocots to a lesser extent than what has been previously believed (papers I, III). Within the group of grasses, several species were found.

Table B5-1. Tundra vole (n=46) preference between grass genera. Results of compositional analysis (see details in paper III) done on a subset of individuals from paper III, including only those which had at least 90% of their total Poaceae consumption at the resolution of genera. The table is read along the rows; there is a ”+” when the genera on a row was used more than the one in a column, and ”-” otherwise. When the difference is significant, the sign is tripled. Genera names are abbreviated to three first letters, full names are *Agrostis*, *Anthoxanthum*, *Avenella*, *Calamagrostis*, *Deschampsia*, *Festuca*, *Nardus*, *Phleum* and *Poa*.

	Agr	Ant	Ave	Cal	Des	Fes	Nar	Phl	Poa
Agr	0	+	—	—	+	-	+++	—	—
Ant	-	0	—	—	+	—	+++	—	—
Ave	+++	+++	0	-	+++	+	+++	+	-
Cal	+++	+++	+	0	+++	+	+++	+	+
Des	-	-	—	—	0	—	+	—	—
Fes	+	+++	-	-	+++	0	+++	+	-
Nar	—	—	—	—	-	—	0	—	—
Phl	+++	+++	-	-	+++	-	+++	0	-
Poa	+++	+++	+	-	+++	+	+++	+	0

Silica-rich genera, i.e. *Deschampsia* and *Nardus* (paper V), are clearly the least preferred food items among grasses. On the other hand, *Calamagrostis* seems to be the most preferred grass genera to feed on. *Calamagrostis phragmitoides* is equally rich in silica as *Deschampsia cespitosa* (paper V), but the silica content of *C. lapponum* and *C. neglecta* (the other species present in the study area) is unknown. No *Calamgrostis* in vole diet data had species level resolution, and it is therefore possible that those species eaten by voles were actually silica-poor.

General discussion and future perspectives

Small rodent population dynamics and plants

Based on my results, small rodent diets are affected by food availability. Both within a habitat and when moving to another habitat, abundantly available food items are more frequently and abundantly consumed. Moreover, when population densities increase, new food items are included in population-level diets. Still, as there seems to be no consistent patterns in which food items are exploited more at higher population densities, we cannot assume that different individuals add the same plants in their diets. Rather, the changes in an individuals diet caused by population density are likely to depend on what is available for different individuals.

Even though these results shed new light on how small rodent diets change during population density cycles, they do not directly point at any single plant taxon. It thus seems unlikely that a plant defence in a single plant species could cause such major changes in rodent mortality or reproduction rate that their population dynamics would be greatly impacted. Rather, the role of induced defences of preferred food plants for small rodents is likely to be manifested through changes in realized food preferences. When the difference in quality between two food items decreases, the profitability of including additional food items in diets evidently increases. A combination of decreased quality of preferred food items together with inclusion of new food items consequently leads to changes in the chemical composition of ingested diet. The impacts of induced defences for rodents are therefore likely to depend on the extent of diet shifts and quality of new food items that are included in diets. The combined intake of different plant defence compounds, in interaction with the intake of nutrients, is more likely to determine an animal's physiological status than the intake of a single compound alone (Villalba et al. 2002; Provenza et al. 2007; Nersesian et al. 2012b). Thus, deeper understanding of the role of food for small rodent population dynamics could be gained by focusing on the compensatory effects of different food items and the combined quality of realized diets.

Majority of the literature around small rodent population dynamics has focused on the mechanisms creating population cycles, while other aspects of population dynamics have received less attention (Angerbjörn et al. 2001; Krebs 2011). However, the pronounced geographical differences in peak population densities of small rodents (Krebs 2011) have major impacts in shaping the different tundra ecosystems. For example, on Bylot Island where peak population densities of lemmings have been recorded to be 20 individuals/ha (paper IV) lemmings seem to consume only a fraction (5%) of the annual biomass production (Legagneux et al. 2012). In contrast, at Point Barrow, Alaska, lemming peak densities may reach above 200 individuals/ha (Pitelka and Batzli 2007) and consequently lemmings have been estimated to remove up to 50% of the vascular plant standing crop (Batzli et al. 1980). In spite of the rather generalist food habits of small rodents (papers I-IV), not all green vegetation (i.e. total productivity) can be considered to be usable food for rodents (paper III).

Spatial variability in small rodent peak population densities at regional scales seems to be little correlated with productivity, although at global scale such a pattern emerges (Batzli and Jung 1980; Jedrzejewski and Jedrzejewska 1996; Ims et al. 2011). Rather than total plant productivity, it seems likely that patterns in the availability of preferred food items would explain regional variation in population cycle properties. Moreover, diversity of small rodent diets has been little studied (but see Sassi et al. 2011), even though it appears to be a potentially important aspect of small rodent feeding ecology (paper III). Combining measurements of food item diversity, both taxonomic and chemical, with those of availability appears therefore as an interesting avenue for new insights to the interaction between vegetation and small rodents.

More generally, incorporating qualitative aspects of food availability into a common framework with quantitative availability should improve our understanding of carrying capacity for herbivore population sizes.

Small rodents and other tundra herbivores

Based on my results on rodent diets, there is a clear potential for both intraspecific and interspecific exploitation competition during population density peaks (papers I-IV, Box 4). In addition to small rodents, semi-domesticated reindeer are abundant herbivores in Fennoscandian tundra ecosystems. Although little data is available on the diet of reindeer, many of the plants that I found to be important in small rodent diets have been indicated to be important for reindeer as well (Bråthen and Oksanen 2001). Several taxa with an important contribution to small rodent diets, such as *Vaccinium myrtillus*, *Avenella flexuosa* and family Polygonaceae are food items frequently grazed by reindeer (Warenberg et al. 1997; Bråthen and Oksanen 2001). Hence, the diet of reindeer most likely overlaps with that of rodents. Such exploitation competition has been even suggested to have caused lack of population density peaks in Northern Fennoscandia during the last decades, with cascading effects on the food web (Kjellén and Roos 2000; Angerbjörn et al. 2001; Ratcliffe 2005).

In other ecosystems, large herbivores have been found to modify both nutritional quality of available vegetation as well as habitat structure to such an extent that small rodent population densities are affected (Suominen and Danell 2006; Saetnan and Skarpe 2006; Austerheim et al. 2007; Bakker et al. 2009; Muñoz et al. 2009). There are currently only two studies evaluating impacts of reindeer on small rodents in tundra habitats, and the results of these studies do not indicate any consequent negative effect (Ims et al. 2007; Henden et al. 2011). The impact of ungulates on small herbivores has in different ecosystems been suggested to be mediated through different processes, such as reduced shelter (Bakker et al. 2009; Muñoz et al. 2009) improved food quality (Austerheim et al. 2007) and reduced food availability (Torre et al. 2007). Such a wide range of potential mechanisms, together with the variability in rodent species food and habitat preferences (this thesis and references within), indicates that the relationship between reindeer and small rodents in tundra habitats probably differs between rodent species as well as habitats. Moreover, spatial variation in food availability (Ravolainen et al. *in revision (a)*; paper III) and quality (Bråthen et al. 2004; DeGabriel et al. 2010; paper V), could explain the spatially variable relationships between rodents and reindeer-modified vegetation indicated by Henden et al. (2011).

Further questions emerging from this thesis

The methodological part of this thesis leads to new possibilities for studies of small rodent feeding ecology. For example, winter is a crucial period for shaping many aspects of small rodents population biology, but the knowledge of rodents winter ecology is currently rather fragmentary (Aars and Ims 2002; Kausrud et al. 2008; Krebs 2011). As snow cover prevents the use of many methods routinely employed during summer, development of methods that enable studies of rodent winter ecology is needed. DNA metabarcoding could provide such new opportunities, by enabling diet analyses from faeces collected after snow melt from rodent winter habitats. Further, the role of fungi for interactions between rodents and plants is largely non-explored. While DNA-based methods open up for taxonomic identification of ingested fungi, the difference in stable isotope ratios of plants and fungi (Trudell et al. 2004) may be useful for determining the abundance of fungi in diets.

Some of the interesting questions emerging from the ecological part of this thesis are those of the relative roles of different drivers for small rodent food selection in the wild, and their consequences for rodent population dynamics. For example, how does predation risk modify food selection? Could increased predation risk and competition during high population densities lead to so unselective feeding that it has consequences for rodent population dynamics? In an other well studied example of population cycles, the Canadian snowshoe hare, predation risk has indeed been found to contribute in creating cyclic dynamics by inducing severe stress (Boonstra et al. 1998; Krebs 2011). It is undoubtedly difficult to differentiate between the effects of stress caused by reduced food quality, predation risk and constrained selectivity for food due to predation risk. In spite of such challenges, I suggest that the non-lethal effects of predation on both herbivore feeding ecology and small rodent population ecology warrant for more research. Moreover, what is the mechanism through which competition impacts small rodent diets? Is the effect of increased population density simply manifested through exploitation competition for changed food availability, or does also interference competition have a role?

Further, grass silica defences probably contribute to the interaction between reindeer and small rodents. It remains, however, to be tested to what extent the different positive and negative interactions discussed under the title ”Role of grass silica defences in tundra food webs” actually take place. Moreover, tundra herbivores probably do interact indirectly also through other plants than silica-rich grasses, but through which plants and what are the consequences of such interactions for these herbivores, remain unanswered questions presently.

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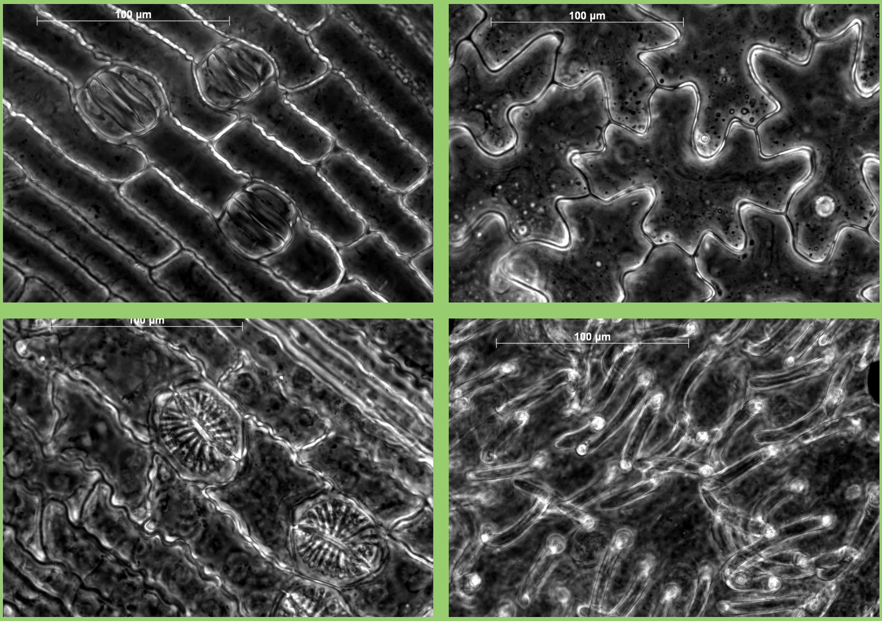

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Paper III. Arctic small rodents have diverse diets and flexible food preferences

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