Summer Feeding Behaviour of Reindeer: A Hierarchical Approach

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Abstract

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Reindeer (*Rangifer tarandus* L.) plays an important role ecologically, economically, as well as culturally in northern Fennoscandia, where reindeer husbandry traditionally has considered winter to be the bottleneck for reindeer. Recent studies have shown that summer feeding conditions control reindeer population dynamics through indirect effects on winter survival and reproductive success.

My thesis is unique as it analyses seasonal plant nutrient dynamics, their spatial patterns and reindeer summer foraging behaviour at different levels simultaneously. The aim was to test the underlying assumptions behind the hypothesis that reindeer select the new emerging growth (highly digestible and protein rich) and move into new areas as the emergence of new growth proceeds along climatic gradients. The studies were done in a mountainous landscape of sub-arctic northern Sweden used by the semi-domesticated reindeer herd belonging to Gabna Sami community.

The study on plant nutrient dynamics of four forage species (*Betula nana* L., *Eriophorum angustifolium* L., *Rumex acetosa* L. and *Vaccinium myrtillus* L.) revealed that plant nitrogen concentrations (and thus protein content) related to snowmelt patterns. It was further shown that reindeer selected areas with high landcover diversity, and thus might respond to any landscape heterogeneity that results from varying snowmelt patterns. Within landscapes, reindeer selected species rich plant communities with high abundance of preferred food plants (deciduous shrubs, herbs and graminoids) and fed where food biomass was high, predominantly that of birch and willow species. Contrary to predictions of the tested hypothesis, it was concluded that reindeer responded to food quantity rather than quality at intermediate (i.e., within plant communities) levels of feeding habitat selection. Feeding habitat selection at higher (i.e., feeding area and plant community selection) and lower (i.e., plant species and parts selection) levels indicated the importance of food quality and was thus in agreement with the tested hypothesis.

My results have implications for land management as they show the importance of maintaining heterogeneous alpine landscapes for reindeer husbandry. Furthermore, reindeer husbandry needs to be practised at a level that maintain species rich and diverse plant communities. These plant communities were shown to be important feeding habitats, at the same time as they may contribute to nature conservation goals.

Keywords: foraging behaviour, nature conservation, plant nutrient dynamics, *Rangifer tarandus*, reindeer husbandry, spatial and temporal patterns, Sweden

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Executive summary in Swedish

Renens sommarbete från en hierarkisk synvinkel

Renen (*Rangifer tarandus* L.) är ett hjortdjur som spelar en viktig ekologisk, ekonomisk och kulturell roll inom de nordiska länderna och Ryssland. Renskötseln har traditionellt uppfattat vintern som en produktionsbegränsande faktor. Nya vetenskapliga rön visar dock att betesförhållandena sommartid påverkar renhjordens tillväxt genom indirekta effekter på vinteröverlevnad och fortplantningsframgång.

Min avhandling är unik eftersom den behandlar säsongsbundna förändringar av växters födokvalitet, dess rumsliga variation och renens sommarbete på flera olika nivåer samtidigt. Avhandlingens syfte var att pröva giltigheten i de bakomliggande antagandena för den dominerande hypotesen om renars födoekologi. Hypotesen förutsäger att renen väljer att beta i den nyuppkomna spirande vårgrönskan (med hög smältbarhet och proteininnehåll) och sedan flyttar till nya betesområden i takt med den framväxande nya växtligheten. Studierna utfördes i ett fjällandskap i norra Sverige inom vår-, sommar- och höstbetesområdena för Gabna samebys renhjord.

Avhandlingen behandlar inledningsvis fyra renbetesväxters (blåbär, dvärgbjörk, ängssyra och ängsull) säsongsbundna förändringar i födokvaliet. Där visas att växternas kvävekoncentration (och därmed växternas proteininnehållet) är relaterad till snösmältningstidpunktens infallande, och stödjer de antaganden som ligger bakom hypotesen om renarnas födoekologi. En annan delstudie visade att renar väljer betesområden av varierande landskapstyp och omväxlande vegetation samt att renar därmed troligen reagerar på landskapsstrukturer skapade av olika snösmältningsförhållanden. Inom ett betesområde valde renarna att beta artrika växtsamhällen med hög förekomst av begärliga betesväxter (gräs, lövfällande buskar och örter). Inom dessa växtsamhällen betade renarna där födokvantiteten var som störst, främst av björk och vide. Sammanfattningsvis reagerade renen på födokvantitet snarare än kvalitet vid valet av födoplats inom växtsamhällen, vilket står i motsats till den allmänna teorin om växtätares födoekologi. Valet av betesområden och växtsamhällen liksom valet av födoväxter och växtdelar antydde dock vikten av födokvalitet för renens betesval vilket var i överensstämmelse med teorin om renars födoekologi.

Mina resultat belyser värdet av att bevara biologiskt omväxlande fjälllandskap för renskötseln och att hänsyn till detta bör tas i den regionala markanvändningsplaneringen. Renskötseln bör vidare bedrivas på ett sådant sätt att den bibehåller artrika växtsamhällen eftersom de är betydelsefulla betesplatser, samtidigt som de kan bidra till att uppfylla viktiga mål för svenskt och europeiskt naturskydd.

Contents

Appendix

Papers I-IV

The present thesis is based on the following papers, which will be referred to by their Roman numerals:

I. Mårell, A., Hofgaard, A. & Danell, K. 2006. Nutrient dynamics of reindeer forage species along snowmelt gradients at different ecological scales. *Basic and Applied Ecology 7*, 13-30.

II. Mårell, A., Ball, J.P. & Hofgaard, A. 2002. Foraging and movement paths of female reindeer: insights from fractal analysis, correlated random walks, and Lévy flights. *Canadian Journal of Zoology 80*, 854-865.

III. Mårell, A. Reindeer habitat selection: Does plant species diversity matter? (Submitted manuscript).

IV. Mårell, A. & Edenius, L. 2006. Spatial heterogeneity and hierarchical feeding habitat selection by reindeer. *Arctic, Antarctic, and Alpine Research 38,* 413-420.

Papers I, II, and IV are reproduced by permission of the journals concerned.

Introduction

Background

Reindeer (*Rangifer tarandus* L.) is a member of the native large-sized herbivore community in northern Fennoscandia (Skjenneberg & Slagsvold, 1968). In modern times, it has been semi-domesticated in Sweden and most parts of Finland and Norway (Lönnberg, 1909; Manker, 1953; Dahle et al., 1999), and in these areas plays an important role ecologically, economically, as well as culturally (Sandström et al., 2003). In Sweden, reindeer husbandry is exclusive to the Sami (although the right of possession is not), and is part of their cultural heritage. Two main modes of reindeer husbandry exist in Sweden. Sami communities bordering the Baltic Sea and Finland, and without alpine areas, keep their reindeer in the boreal forests all year round. Sami communities further to the west, bordering Norway, let their reindeer migrate between the winter ranges in lowland boreal forests and the summer ranges at high altitudes in the Scandinavian mountains. Traditionally, reindeer husbandry has mainly considered winter ranges to be the bottleneck for reindeer husbandry. Although winter feeding conditions are harsh and can cause high winter mortality (Gates, Adamczewski & Mulders, 1986), summer feeding conditions have been demonstrated to control reindeer population dynamics (Post & Klein, 1999) through indirect effects on winter survival (White, 1983) and reproductive success (Tveraa et al., 2003). A better understanding about the reindeer's habitat requirements and what constrains feeding habitat selection of reindeer during summer is therefore important and needs to be incorporated into reindeer management plans.

Reindeer ecology

Reindeer/caribou has a circumpolar distribution from the boreal forest region to the high Arctic (Williams & Heard, 1986; Klein, 1996; Røed, 2005). It belongs to the deer family (Cervidae) and is classified as a grazer/browser that is intermediate between bulk feeders and concentrate selectors (Hofmann, 1989; Hanley, 1997). The diet is highly mixed (White et al., 1981; Baskin & Danell, 2003), and reindeer/caribou adapt their diet to local conditions (Leader-Williams, Scott & Pratt, 1981; Staaland et al., 1993). In general, the diet of reindeer/caribou changes from being energy-rich and lichen-dominated during winter (Heggberget, Gaare & Ball, 2002), to become protein-rich and dominated by herbs, shrubs and grasses during summer (Gaare & Skogland, 1975; Nieminen & Heiskari, 1989; Klein, 1990). This coincides with the annual physiological cycle of reindeer/caribou with stagnated growth and body maintenance during the winter half, and high nutritional demands for protein to support growth and lactation during late spring and summer (Klein, 1990).

Across their distribution range, wild reindeer/caribou are either stationary or migrate between seasonal ranges. Migration mainly follows latitudinal or altitudinal gradients. Modern reindeer husbandry in the Scandinavian mountain chain follows these natural migration patterns. Three major hypotheses have been proposed to explain the migratory behaviour and seasonal habitat selection observed among reindeer/caribou during the plant growing season: (i) the high-quality-food-seeking hypothesis (throughout the plant growing season), (ii) the predator-avoidance hypothesis (at the time of calving), and (iii) the parasite-avoidance hypothesis (post-calving migration).

The high-quality-food-seeking hypothesis

It is hypothesised that reindeer/caribou select new emerging plant growth, which is of high nutritional value, and move into new areas as the emergence of new growth proceeds along climatic gradients (Klein, 1970; Skogland, 1980). This hypothesis is supported by comparative studies that have shown a positive correlation between plant phenology, and population dynamics and characteristics of northern ungulates (Albon & Langvatn, 1992; Langvatn et al., 1996; Post & Stenseth, 1999).

The predator-avoidance hypothesis

Spring migration is, however, characterised by sexual segregation where female reindeer/caribou starts migration earlier than males (Baskin & Danell, 2003; personal observations), and where pregnant females have been observed to precede the emergence of new plant growth (Whitten & Cameron, 1980; Fancy & Whitten, 1991). Similarly, Bergerud, Butler and Miller (1984) observed that caribou females in northern British Columbia migrated at the time of calving to high alpine areas poor in food species and with low food quantity in order to reduce the risk of calf predation. Once the calves were 2-3 weeks old, they moved back into areas with high food quality and quantity. It has therefore been suggested that early spring migration and habitat selection of female reindeer/caribou are related to and constrained by the risk of predation (Bergerud & Elliot, 1986; Bergerud & Page, 1987; Bergerud, 1996).

The parasite-avoidance hypothesis

Later during the summer, reindeer/caribou use specific habitats, relief areas (e.g., ridges, snowpatches, sandy patches, marshland and shallow water), more frequently during severe insect harassment (Gaare, Thomson & Kjos-Hanssen, 1975; Downes, Theberge & Smith, 1986; Walsh et al., 1992; Toupin, Huot & Manseau, 1996). However, it is still unclear whether this relief area selection is entirely due to insect harassment, or partly to thermoregulation (Ion & Kershaw, 1989; Walsh et al., 1992; Andersen & Nilsen, 1998). Some of these relief habitats are typical for high altitudes (e.g., mountain ridges and snowpatches) or coastal ranges (e.g., wind-exposed shores and shallow water); areas to where reindeer/caribou migrate after calving. Furthermore, the time when important parasites such as warble fly (*Hypoderma tarandi* L.) seek new hosts coincides with that of calving. By migrating into new areas after calving, reindeer reduce the levels of parasite infection (Folstad et al., 1991). Insect harassment (or thermoregulation) and parasite avoidance have therefore been proposed as possible explanations for the post-calving migration observed among reindeer.

Objectives

The main objective of my thesis focus on the first hypothesis, and in particular to study summer foraging behaviour of reindeer in relation to seasonal dynamics and spatial patterns of potential food resources. My ambition was to provide basic knowledge that could be used to quantify feeding habitat characteristics of mountain reindeer which could be incorporated into reindeer management plans. More specifically, papers I-IV deal with aspects of nutrient dynamics of reindeer forage species and reindeer foraging behaviour.

Paper I - To quantify temporal and spatial plant nutrient dynamics in alpine sub-arctic environments in order to test whether this pattern of food plant quality conform to an evolutionary adaptive behaviour where reindeer track the new emerging growth throughout the plant growing season.

Paper II - To evaluate the importance of food quantity and quality to selection of feeding stations by reindeer through studies of movement patterns and feeding behaviour of female reindeer during foraging bouts.

Paper III - To study feeding plant community selection of reindeer in order to quantify important summer feeding habitats of reindeer.

Paper IV - To deduce habitat characteristics at three different spatial levels aiming at describing qualitative structures of the landscape important for feeding habitat selection of reindeer during the plant growing season.

Theoretical frameworks

Alpine and sub-arctic plant nutrient dynamics

In addition to inter-specific differences in plants, concentrations of mineral nutrients in plant tissues are mainly related to nutrient supply and growth dynamics (Chapin, Van Cleve & Tieszen, 1975; Chapin, Johnson & McKendrick, 1980). In the early growing season, concentrations of mineral nutrients increase due to relatively higher rate of nutrient allocation than growth rates (Mengel & Kirkby, 1987). Thereafter, these concentrations in leaf and stem tissues decrease (1) through dilution due to the accumulation of carbon (rapid growth and maturation processes), and because of (2) retranslocation of nutrients to reproductive organs, and (3) recovery of nutrients during senescence (Mengel & Kirkby, 1987; Körner, 1999). Thus, plant nutrient quality, in terms of forage for herbivores, is high at the beginning of the plant growing season and successively declines as the plant growing season proceeds. Another important factor for nutrient dynamics of alpine and sub-arctic plants is the leaf life span, which is a function of growing-season length and that controls nutrient concentrations of plant tissues along snow-retreat gradients, i.e., altitude gradients (Körner, 1989) and melting snowpatches (Kudo, Nordenhäll & Molau, 1999). The onset and length of the plant growing season in alpine and sub-arctic ecosystems depend on snow distribution patterns (Billings & Bliss, 1959; Schaefer & Messier, 1995; van Wijk et al., 2003). Alpine and sub-arctic tundra ecosystems, thus provide environmental gradients wherein different snowmelt regimes at small and large scales are expected to cause complex spatio-temporal patterns of plant nutrient dynamics, and to which animals may have adapted their foraging behaviour.

Feeding habitat selection

A hierarchical strategy

Habitats contain environmental resources needed for animals to grow, reproduce and survive (Hall, Krausman & Morrison, 1997), but also for their competitors (Fretwell, 1972) and predators (Lima & Dill, 1990). These resources, competitors and predators are generally unevenly distributed in time and space (Bryant, 1973; Wiens, 1976; Orians & Wittenberger, 1991; Levin, 1992), which gives rise to habitat quality differences (Charnov, 1976). Thus, some habitats have greater availability and quality of food (Nellemann & Thomsen, 1994), while other habitats differ in inter- and intraspecific competitors (Hughes, Ward & Perrin, 1994; Klein & Bay, 1994), predation risk (Bergerud, Butler & Miller,1984), the probability of finding mates (Cransac & Hewison, 1997), or the potential to successfully rear young (Spitz & Janeau, 1995). Animals are therefore expected to select habitats according to their quality versus their costs and benefits (Festa-Bianchet, 1988; Lima & Dill, 1990; Mauritzen et al., 2003), given that they conform to behaviours that have evolved by adaptation (Parker & Maynard Smith, 1990). Food is one of the most important resources for the growth, reproduction and survival of animals. Consequently, animals such as generalist herbivores respond to spatial and temporal variability of food availability by selecting specific feeding habitats (McNaughton, 1990; Wilmshurst et al., 1999; Ball, Danell & Sunesson, 2000) and diet (Hanley, 1997; Dumont, Carrère & D'Hour, 2002). The decision process of habitat selection can be viewed as a hierarchical process (Johnson, 1980), where selection occurs at (i) high levels (e.g., region, landscape or home range/territory), (ii) intermediate levels (e.g., feeding area, patch or plant community), and (iii) low levels (e.g., feeding site/station, micropatch, plant species or plant part) (Senft et al., 1987).

Foraging theory

Conventional foraging theory (Optimal Foraging Theory, OFT; Emlen, 1966; MacArthur & Pianka, 1966) was originally developed to make predictions about what, where and when predators would eat (Pyke, Pulliam & Charnov, 1977; Perry & Pianka, 1997). Maximisation of net rate of energy gain, and that animals thereby maximise their long-term reproductive success, were the main assumptions associated with these early models (Stephens & Krebs, 1986). Animals would then behave (i.e., select feeding habitats and diet) as to either fulfil a minimum energy requirement and thereby minimise the time spent feeding (time minimizer) or maximise the net energy gain for a given time spent feeding (energy maximizer) (Schoener, 1971). Feeding of generalist herbivores, such as ruminants, is somewhat different from that of predators. Searching and handling (ingestion and digestion) of food are not mutually exclusive activities for ruminants, but rather overlap with complicated feedback mechanisms (Hanley, 1997), where dry-matter intake rate increases asymptotically and relates to bite and leaf size (Spalinger & Hobbs, 1992; Gross et al., 1993). For deer grazing in pastures, dry-matter intake rate is correlated with food biomass (Wickstrom et al., 1984), but not for deer browsing shrubs (Spalinger & Hobbs, 1992; Gross et al., 1993). Furthermore, the diet of ruminants is complex and composed of many plant species, some of which are nutritious, and some that contain toxic compounds. Several hypotheses have been proposed to explain the mixed diet and foraging selection of generalist herbivores. Stephens and Krebs (1986) classified them in the following groups: (1) rate maximising subject to nutrient constraints, (2) selecting complementary nutrients, and (3) avoiding toxins. These models predict diets and selection of feeding units within the limits of constraints intrinsic to the foraging process, such as body size and digestive morphology (Bell, 1970; Hofmann, 1973; Jarman, 1974; Demment & van Soest, 1985; Illius & Gordon, 1990), as well as external constraints such as competition (Fretwell, 1972) and risk of predation (Lima & Dill, 1990).

Animal movement

Animal movements in relation to the spatial distribution of environmental resources occur at different hierarchical levels (Hassell & Southwood, 1978). At high levels, animals migrate between different home ranges, territories or habitats, while they range between patches and actively search within patches at lower levels (Bell, 1990). When resources are beyond the animals' sensory-detection range, animals can improve their search efficiency by using their spatial memory (Bell, 1990) or adopt a random search behaviour that involves extremely long moves (i.e., movement lengths follow an inverse square power-law distribution, a characteristic of Lévy flights) (Viswanathan et al., 1999). When resources are within the animals' sensory-detection range, OFT predicts that animals should stay and feed in patches for a longer time (i.e., "area-restricted search") when they encounter patches with higher food quality (Charnov, 1976). Bell (1990) described five major mechanisms of area-restricted searching that animals could utilise when they encounter a profitable foraging area: (i) looping or spiralling as a result of a turn bias, (ii) increasing the frequency of turning right and left, (iii) decreasing movement length, (iv) changing arrival-departure directions, and (v) turning back when profitability decreases below a critical threshold ("patch-edge recognition"). These area-restricted search behaviours all result in a non-random movement pattern that increases search efficiency.

Material and methods

Study area

The study was done in a mountainous landscape of sub-arctic northern Sweden including Abisko National Park (68˚19'N, 18˚40'E). The study area (2100 km^2) was defined by the spring, summer and autumn ranges used by the semi-domesticated reindeer herd belonging to Gabna Sami community (Fig. 1). The area is characterised by a strong climatic gradient over short distances with prevailing oceanic influences in the west and continental influences in the east (Andersson, Callaghan & Karlsson, 1996). The long-term average (1961-90) of annual mean temperature at Abisko Meteorological Station (68˚21'N, 18˚49'E, 388 m above sea level) is -0.8˚ C, and mean temperature of the warmest month, July, is 11.0˚ C (Alexandersson, Karlström & Larsson-McCann, 1991). The elevation in the area ranges from 332 to 1803 m (25% of the study area is >1000 m), with the highest mountains in the western parts. The tree line formed by mountain birch, *Betula pubescens* ssp. *czerepanovii* (Orlova) Hämet-Ahti, runs at approximately 550-600 m in the west and 700-800 m in the east. Valleys below tree line have mountain birch forests, mixed with open fens and sub-alpine heaths (Berglund et al., 1996). The low alpine belt above the tree line has heaths dominated by dwarf shrubs such as *B. nana* L., *Vaccinium myrtillus* L. and *Empetrum nigrum* L. (Sjörs, 1999), and patches of willow (*Salix* spp.). The middle alpine belt is characterised by graminoid and herb dominated communities; the prevalent species are *Carex bigelowii* Torr, *Calamagrostis lapponica* (Wahlenb.) Hartm., *Juncus trifidus* L., *Ranunculus acris* L., *Viola biflora* L., and *Rumex acetosa* L. The high alpine belt above approximately 1100 m has discontinuous plant cover (Sjörs, 1999).

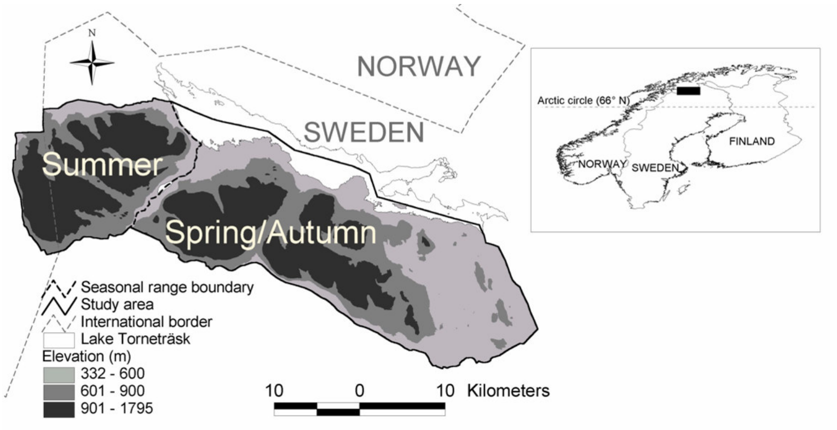

Fig. 1. The study area comprising the entire summer (600 km^2), and spring and autumn (1500 km^2) ranges for the reindeer herd belonging to Gabna Sami community, N Sweden.

Study design

The summer feeding behaviour of reindeer was studied by analysing (i) spatial and temporal plant nutrient dynamics of selected reindeer forage species (Paper I), and (ii) feeding units selection through a hierarchical approach at the levels of feeding station (Paper II), plant community (Paper III) and feeding habitat (Paper IV) selection.

Nutrient dynamics of reindeer forage species (Paper I)

Nutrient dynamics of four reindeer forage species (*Betula nana*, *Eriophorum angustifolium* L., *Rumex acetosa* and *Vaccinium myrtillus*) were studied at four ecological scales: (1) season, (2) prevailing climate, (3) altitude, and (4) snow-patch retreat (Paper I). Study sites were sampled throughout the growing season (scale 1: seasonality). Two altitudinal gradients were selected representing early and late seasonal snowmelt. One gradient was allocated to the continental eastern part of the study area with low winter precipitation, and the other to the oceanic western part with high winter precipitation (scale 2: prevailing climate). Study sites were selected at 500, 700, 900, and 1100 m elevations along the gradients (scale 3: altitude). In the summer of 2000, two additional sites were selected at 500 and 900 m in both the continental and oceanic area to estimate the among-site variability at the same elevation. Furthermore, the within-patch variability of plant nutrient concentration (scale 4: snow-patch retreat) was studied in the summer of 2000 along snowmelt gradients at three snow-patches at 500 m. Two snow-patches (A and B) were located in open birch forests and a third one (C) was on a sub-alpine heath.

The quality of plants as food for herbivores varies with their concentrations of (i) certain important metabolisable nutrients (e.g., energy, protein and phosphorus), (ii) digestibility-reducing substances (mostly cell-wall constituents), and (iii) toxins (e.g., alkaloids and cyanogenic glycosides). Plant nitrogen concentration was used as it is often used as an index of plant quality because it positively correlates to plant protein content and dry matter digestibility (Robbins, 1993), i.e., an index of digestible energy (Wilmshurst & Fryxell, 1995). Digestible energy and protein are the nutritional factors most likely to restrict herbivores in their daily food intake (Robbins, 1993). Phosphorus and plant fibre were also used as they are other important nutritional factors (Robbins, 1993).

Animal foraging behaviour (Papers II, III and IV)

Reindeer herding is traditionally divided into eight seasons in Scandinavia (Sandström et al., 2003). Observations of reindeer foraging behaviour were made from end of May to early September, thus, covering three of these eight seasons: a) end of May to early July (hereafter "late spring"), b) July ("summer"), and c) August to early September ("early autumn"). In the study area, passing from one season to another was marked by herding interventions moving the reindeer herd westward from the spring to the summer range across Abisko river, and eastward from the summer to the autumn range, respectively (Fig. 1; Niia, 1986). Within seasons, reindeer were left to graze freely. Analyses of feeding unit selection followed this division because between-seasonal movements were mainly caused by humans and were thus excluded from analyses, while within-seasonal movements were considered as independent of herding activities and thus to reflect feeding unit selection behaviour by reindeer.

Eight female reindeer were equipped with radio collars (TXE-3 Televilt International AB, Lindesberg, Sweden) in July 1998. They were used to facilitate the observation of reindeer foraging behaviour. Groups and individuals of reindeer were approached by using available cover and were observed from a distance so that animals were not disturbed. No reindeer was observed more than once during the same day, and groups of reindeer were considered as single observation units to ensure statistical independence. Only observations of reindeer displaying feeding behaviour as dominant behaviour were used in order to reflect feeding unit selection. Animals were observed and geographically positioned with the help of laser range-finding binoculars (Leica Vector 1000, Leica Geosystems AG, Heerbrugg, Switzerland). Field observations were carried out during three consecutive plant growing seasons: from 1998 to 2000.

Feeding station selection (Paper II)

Foraging female reindeer were observed with the help of laser range-finding binoculars for a maximum of 30 min, and distance and azimuth were recorded every 30 seconds to precisely establish the position of the reindeer in relation to observed behaviour. Behaviour was recorded in six classes: grazing (head down while standing or walking), browsing (head moving up and down while standing or walking, indicating stripping of leaves from shrubs and trees), lying, standing, walking, and running. Vegetation analyses were performed where reindeer displayed feeding (feeding station) and non-feeding behaviours. Plant species composition was recorded, and all aboveground green biomass was collected to estimate the dry matter weight of potential food items (four plant groups: ericaceous species, deciduous woody plants, graminioids and herbaceous species) as well as their nitrogen concentration.

Feeding plant community selection (Paper III)

The study area was divided into two parts, which correspond to the seasonal use of reindeer and herding activities. Reindeer habitat use was evaluated by a survey of randomly located 2-km line transects (n = 9) during the plant growing season 2000. Reindeer were systematically observed when walking along the line transects as well as walking from one line transects to another. Both types of observations of reindeer were included in analyses. Plant species composition was recorded within circular plots (100 m^2) at places where reindeer were observed to feed (hereafter "used" plant communities), as well as along line transects at every 400 m ("available" plant communities), thus a maximum of 5 plots per transect. Within these circular plots three randomly placed 5-m line transects were placed and used for field layer (vascular plant species) and bottom layer (lichen, moss, litter, bare soil, stone, water or snow) recordings (one point recording every 10 cm) along the line. Recorded vascular plant species were grouped into cryptogams, graminoids, herbaceous species, deciduous and evergreen woody plants species, in order to reflect differences between species with regard to cropping behaviour (grazing or browsing) and nutritional content.

Feeding habitat selection (Paper IV)

Feeding habitat selection was evaluated by a two-step hierarchical process. First, habitat selection was analysed at a coarse scale (5-km grid size) using the whole study area as defining available habitat. Second, habitat selection at finer scales (0.5 and 1-km grid size) was evaluated assuming that reindeer had selected feeding area at a higher spatial scale: i.e. using the 5-km grid cells where reindeer was observed to delineate the amount of hypothetically available habitats (number of grid cells). Principal Component Analysis (PROC FACTOR, SAS Institute Inc. Ver. 8.2) was used to derive major uncorrelated environmental factors influencing the spatial pattern of topography and land cover characteristics (Manly et al., 1993). These principal component factors were then used to analyse reindeer feeding habitat selection.

Results and discussion

Nutrient dynamics of reindeer forage species (Paper I)

Temporal patterns

Nitrogen and phosphorus concentrations peaked between the middle of June to the end of July, depending on species, altitude and area (Paper I). Delayed timing of peak nutrient concentrations within plant species correlated with snowmelt patterns, well in agreement with the underlying assumptions of the high-quality-food-seeking hypothesis. Not only the timing, but also the level of nutrient concentrations were related to snowmelt patterns, and generally reached higher concentration levels in plants at sites with late snowmelt. The largest differences in nutrient concentrations were between plant species (Paper I), both in magnitude (with as much as a 6- and 10-fold difference for nitrogen and phosphorus, respectively) and in the timing of peak concentrations (3-4 weeks). Such large differences in food quality between species and plant parts have been observed in previous studies of reindeer forage species (Gaare & Skogland, 1975; Nieminen & Heiskari, 1989; Klein, 1990). These marked differences between species could result in a strong feeding selection at the level of plant species (and plant communities). Furthermore, apparent seasonal trends in nutrient quality among the studied reindeer forage plant species were observed (Paper I). These seasonal changes explained most of the observed variability in plant nutrient quality within species and are in agreement with findings from other tundra areas (Chapin, Van Cleve & Tiezen, 1975; Chapin, Johnson & McKendrick, 1980). The spatial variability of nutrient concentrations was much lower than differences between plant species and seasonal changes (Paper I). This suggests that foraging reindeer would show more selectivity across the temporal scale, rather than across the spatial scales studied, given that the nutritional requirements are approximately the same throughout the study period. These results agree with the high seasonal changes in diet observed for reindeer (Gaare & Skogland, 1975; White et al., 1981).

Spatial patterns

Differences in plant nutrient concentrations and timing of peak concentrations within plant species were lower than expected across snowmelt gradients, and showed inter-specific patterns. A general trend of increasing nitrogen concentration along snowmelt gradients at low (within snowpatches) and medium (altitude) spatial scales were observed, but not between the two areas with early and late snowmelt (Paper I). For species such as *Vaccinium myrtillus* that grow in patches with a varying length of snow cover duration, variability in plant nitrogen and phosphorus concentrations were as large within patches as among altitudes and between the two areas with different snowmelt regime. Such a spatial pattern of plant nutrient variability suggests that alpine sub-arctic areas can provide heterogeneous environments within a rather small area wherein a selective herbivore such as reindeer could find patches containing plant species with progressive emergence of early growth stages. It further suggests that reindeer do not necessarily need to migrate into new areas or follow the snow retreat along an altitude gradient, but rather could remain stationary. However, other plant species such as *Eriophorum angustifolium* with another ecological niche (i.e., a narrow ecological niche with regard to snowmelt regimes) do show a spatial variability, although weak, that could support an adaptive behaviour of reindeer moving between areas (or altitudes) with early and late snowmelt.

Reindeer foraging behaviour

Feeding station selection (Paper II)

Reindeer selected feeding stations during foraging bouts that had higher green biomass, predominantly birch and willow species, than non-feeding stations (Paper II). Selection of feeding stations based on nitrogen concentration of preferred food plants was, however, not observed (Paper II). These results indicate that food quantity rather than food quality is more important at the level of feeding station selection, which also has been shown for Svalbard reindeer (van der Wal et al., 2000). This might be explained by low food biomass in the study area (Paper II), which was equivalent to the lower range of biomass values used by Trudell and White (1981) in their food-intake trials with reindeer. Their food-intake trials show increasing food-intake rate with increasing food biomass. In the study area, as well as in similar alpine and sub-arctic environments, reindeer are therefore expected to significantly increase their food-intake rate by selecting feeding stations with higher food biomass. This relationship is likely to be valid for deer grazing in pastures (or alpine meadows resembling grass pastures), as bite size is highly correlated with biomass for grass pastures (Wickstrom et al., 1984). Dry-matter intake rate of reindeer does not correlate with biomass but with leaf size when browsing deciduous woody plants (Spalinger & Hobbs, 1992; Gross et al., 1993). Selection of feeding stations for browsing is therefore expected to be based on leaf size rather than biomass of browse. Selection of feeding stations with high biomass of deciduous shrubs might therefore reflect a threshold value of minimum biomass of browse (Paper II), above which it is profitable for reindeer to feed. However, the functional response and associated feeding mechanisms for reindeer feeding on for example dwarf shrubs such as *Betula nana* are poorly understood, and probably differ from that of deer browsing trees and shrubs for which models of functional responses have been developed (Spalinger & Hobbs, 1992) and tested in the wild (Pastor et al., 1999; Nordengren & Ball, 2005).

Auto- and cross-correlation coefficients of movement length and turning angle for all the recording sequences were generally not statistically significant for any tested time lag (Paper II). This indicates that reindeer were not employing area-restricted search behaviour in contrast to predictions of optimal foraging theory. This conclusion is consistent with observations by Ball, Danell & Sunesson (2000), who found no clear evidence of patch-edge recognition by moose, reindeer, or other herbivores in a manipulative field experiment. Neither Ward and Saltz (1994) nor Focardi, Marcellini and Montanaro (1996) found any correlation between turning angles and food density, which is also in agreement with the results in this study. However, Ward and Saltz (1994) observed shorter movements in areas of high food density for dorcas gazelles (*Gazella dorcas*), and Focardi, Marcellini and Montanaro (1996) reported patch-edge recognition by fallow deer (*Dama dama*).

Foraging paths of reindeer were not totally random walks (i.e. Brownian motion). The tortuosity (measured by the fractal dimension) of the paths was much less than expected for Brownian motion (fractal dimension = 2), and the frequencies of turning angles were non-uniformly distributed (Paper II). It has been proposed that correlated random walks, instead of Brownian motion, should serve as null hypothesis when analysing animal movement paths (Turchin, 1996). The foraging paths in this study met the basic assumptions of a correlated random walk (Kareiva & Shigesada, 1983): specifically, independence between movement length and turning angle (no cross-correlation was found) and symmetric distribution of turning angles around 0º (i.e., an equal probability of turning left or right). However, the discrepancy between the observed net squared displacement and that expected from a correlated random walk suggests that the searching behaviour of the studied reindeer was not made up of independent processes (i.e., it was not a Markov chain). No autocorrelation of movement length and turning angle was found, which could otherwise explain the observed deviation from a correlated random walk. The higher directionality that was observed could be explained by the reindeer following terrain features (e.g., grazing along a slope), or by a tendency to move against the wind due to insect harassment (White et al., 1981). The discrepancy could also be explained by the higher frequency of long movements that was observed (i.e., the distribution function of movement lengths was as predicted for foragers using Lévy flights to search for patchily-distributed food beyond sensory range).

The frequency distributions of movement lengths during foraging resembled the distribution function of Lévy flights, which means that extremely long movements occurred more often than would be expected if reindeer exhibited movement lengths with a normal distribution (Paper II). This observed long-range search pattern is similar to the optimal search strategy that Viswanathan et al. (1999) proposed for foragers dealing with sparsely and randomly distributed food items. It suggests that the reindeer in my study adopted this search strategy when the food items were outside their sensory-detection range; one that would have brought the reindeer into new and unexploited areas with a higher probability than using other search strategies.

Feeding plant community selection (Paper III)

Reindeer fed in species rich and diverse plant communities with high abundance of herbs, deciduous shrubs and graminoids (Paper III), in agreement with other studies on reindeer diet selection and feeding habitat selection in similar alpine environments (Gaare & Skogland, 1975; Skogland, 1980, 1984). However, reindeer did not feed in snowbed environments (light grazing by individuals did, however, occur but groups of reindeer with feeding as their dominant behaviour did not, personal observations). This was somewhat unexpected, as snowbed environment has been reported to be important feeding habitats during summer (Gaare & Skogland, 1975; Skogland, 1984). It was further surprising as Edenius et al. (2003) found snowbed environment to be important habitats for reindeer during spring and summer in the same study area. However, their study was based on faecal pellet counts, and did not associate habitat use with behaviour. The present study suggests that reindeer do not select snowbed environment primarily as a feeding habitat during the plant growing season. Snowbed environment might, however, be important habitats for reindeer during the plant growing season, but for other reasons than feeding. Still, snowbed environment might receive light to moderate feeding while reindeer are on passage from snowpatches (as refuges from insect harassment/thermoregulation) to preferred feeding habitats, which might explain the contradictory results with other studies.

Reindeer has a diverse summer diet (Gaare & Skogland, 1975), and correspondingly fed in plant communities with high species richness and diversity (Paper III). Likewise, Skogland (1980) found that reindeer fed in plant communities with highest species diversity across an alpine gradient. A mixed diet, as found among generalist herbivores such as ruminants, has been proposed to facilitate the digestion of food rich in plant secondary compounds (Freeland & Janzen, 1974; Provenza et al., 2003). Consequently, secondary compounds that are either toxic or digestibility reducing have been observed to affect diet selection of ruminants (Bryant & Kuropat, 1980; Dearing, Mangione & Karasov, 2000). Most of the summer diet of reindeer is highly digestible, although leaves of certain graminioids and woody plants have reduced digestibility and contain toxic compounds (Nieminen & Heiskari, 1989; Klein, 1990; Riipi et al., 2004). Rather than being the primary cause for feeding habitat selection, a diverse diet might only be a reflection of a non-selective food intake in diverse plant communities, where these diverse plant communities primarily have been selected because they maximise the dry matter nutrient intake.

Feeding habitat selection (Paper IV)

Reindeer fed in areas at middle to high elevation with high spatial heterogeneity (Paper IV) in agreement with findings from other similar tundra and alpine environments (White et al., 1981; Skogland, 1989; Nellemann & Cameron, 1996). Habitat heterogeneity and terrain ruggedness were the two most important factors explaining reindeer feeding habitat selection at the landscape level (Paper IV). At a coarse scale (i.e., 5-km grid size), reindeer selected feeding areas with high habitat heterogeneity and terrain ruggedness while avoiding lowland plain environments throughout the study period (Paper IV).

Early in the season (late spring), feeding area selection based on elevation and environmental heterogeneity may result from predator avoiding behaviour during the early post-calving period (Bergerud, Butler & Miller, 1984; Skogland, 1989), which also has been observed among bighorn sheep in alpine environments (Festa-Bianchet, 1988). It might equally be due to the fact that reindeer track the new emerging plant growth (Klein, 1970; Skogland, 1980, 1984), which is high in nutritive quality (Paper I). Rugged terrain in alpine environments give rise to complex snowmelt patterns that in turn have created the heterogeneous landcover mixtures that reindeer selected for. Such a spatial pattern with patches with early and late snowmelt thus contains plants in early growth stages during a longer period than more homogeneous areas (Paper I).

Later in the season (summer and early autumn), reindeer find themselves in a trade-off situation. On the one hand selecting refuge habitats (low in forage) due to insect harassment/high temperature (Ion & Kershaw, 1989; Walsh et al., 1992; Folstad et al., 1991; Andersen & Nilsen, 1998), but on the other hand selecting alpine snowbeds, meadows and heath communities (Paper III; Skogland, 1980, 1984; Edenius et al., 2003) for their higher forage quality and quantity while increasing exposure to parasites. Thus, by selecting feeding areas that are heterogeneous in the sense that they are rich in both refuge and feeding habitats, reindeer could reduce their energetic costs through decreased movements between these two opposing but preferred habitat categories.

At finer scales (i.e., 0.5 and 1-km grid size), seasonal shifts in habitat use were observed (Paper IV). During spring, reindeer habitat selection was positively correlated with terrain ruggedness and habitat heterogeneity and negatively correlated with alpine environment. These results support both behaviours where reindeer seek to avoid predators as well as high quality food, as discussed above. In contrast, reindeer summer feeding habitat selection was negatively correlated with terrain ruggedness and habitat heterogeneity, and positively correlated with southward exposed habitats. This result indicates that reindeer at this level select for nutritive values such as homogenous habitats with constant and predictable food intake rates. A behaviour that was observed in Papers II and III where reindeer selected plant communities with high abundance of food plant species and within these plant communities selected to feed where food biomass was high. The selection of feeding habitats was less pronounced during autumn and differed markedly from that during spring and summer (Paper IV). Such a fine-grained pattern of perceiving the environment might be due to changes in the spatial distribution of potential food resources. This corresponds to the observed changes in searching behaviour where reindeer made longer moves than during spring and summer between each stop for food intake (Paper II). Reindeer shift their diet during early autumn, and one major difference is a preference for mushrooms (Gaare & Skogland, 1975). Perhaps some of the observed changes of reindeer foraging behaviour may have been a result of the fact that mushrooms are spaced differently (i.e., more clumped) than other foods in the area.

Conclusions

Existing ideas about reindeer foraging and habitat use

My thesis shows that current ideas about reindeer ecology describe foraging behaviour of reindeer and the spatio-temporal changes of its food resource in a rather simplistic way. Furthermore, the hypotheses that have been proposed to explain migratory behaviour, within seasonal movements and habitat selection do explain specific aspects of reindeer ecology, but they have so far not been put together in a unifying theoretical framework. My thesis has not treated the whole complexity of reindeer ecology and I will therefore neither be able to propose a new unifying theoretical framework. I will, however, attempt to propose refinements of the current theoretical framework by relating the knowledge about reindeer diet selection with that of other important aspects of reindeer summer ecology. In particular, I refer to the risk of predation and insect harassment as the two most important aspects of reindeer summer ecology other than diet. Further studies are, however, needed that specifically address the seasonal changes in trade-offs between diet selection, predation risk and insect harassment in order to quantify their relationships.

A refined theoretical framework

Results combined for all four studies suggest that reindeer select for a high protein intake during the plant growing season (Fig. 2). However, feeding habitat selection might be constrained by fitness-reducing factors such as risk of predation and insect harassment (Table 1). Reindeer can maintain a high protein intake throughout the plant growing season by feeding in plant communities with high abundance of food resources that are high in protein (i.e., high nitrogen concentration) and by switching plant communities as the protein content of dominant plant species changes due to phenological developments. Results from my studies show that deciduous shrubs and trees are the dominant food resource during late spring, which contain the highest levels of protein. While alpine meadows that are rich in herbs and graminoids are more important during summer as they have higher mean protein content than browse during this period (Fig. 2). During early autumn, reindeer may select between two strategies (Fig. 2): either (i) to feed at very high altitudes where still early growth stages can be found but at low food densities, or (i) to move back down to lower elevations seeking mushrooms in nearby forest ecosystems.

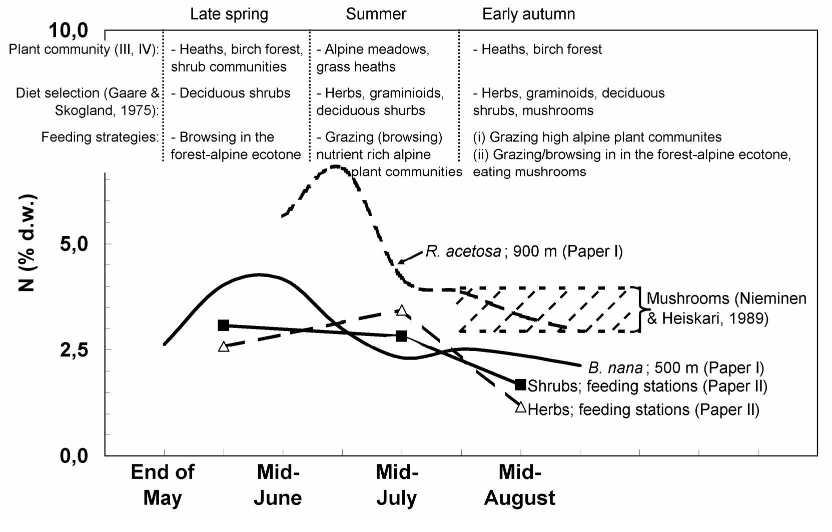

Fig. 2. Seasonal nitrogen concentrations in leaves of *Betula nana* at 500 m elevation and leaves of *Rumex acetosa* at 900 m (Paper I), as well as mean nitrogen concentrations of deciduous shrubs and herbs in plant communities at feeding stations (Paper II).

Table 1. Principal selection criteria explaining migratory patterns and feeding unit selection of reindeer during the plant growing season as well as associated observed behaviours

Behavioural process	**Principal selection criteria**	**Observed behaviours**
Migration and dispersal	- Increased access to high quality food - Reduced predation risk (at the time of calving) - Reduced number of parasites (post-calving) - Reduced competition (early autumn)	- Latitudinal and altitudinal migration (White et al., 1981; Skogland, 1984; Baskin, 1986) - Specific calving grounds (Bergerud, Butler & Miller, 1984; Skogland, 1989; Fancy & Whitten, 1991; Ferguson & Elkie, 2004) - Post-calving migration (Folstad et al., 1991) - Reduced group sizes and dispersal during early autumn (Skogland, 1989)
Habitat selection	- Access to high quality feeding areas - Access to predator refuge areas - Access to insect relief areas	- Selection of heterogeneous environments (Paper IV, Nellemann & Thomsen, 1994) - Use of habitats related to specific behaviours such as feeding (Paper III, IV), parasite avoidance/thermo-regulation (Ion & Kershaw, 1989; Walsh et al., 1992; Andersen & Nielsen, 1998)
Plant community selection	- Abundance of nutrient rich food items - Species composition	- Seasonal changes and selection of plant communities with high abundance of food items rich in nutrients (Paper III; Skogland, 1980)
Feeding station selection	- Biomass and growth form of preferred food items	- Use of feeding stations with high abundance of preferred forage (Paper II; Post & Klein, 1996; van der Wal et al., 2000)
Plant species and plant parts selection	- Nutrient concentration - Digestibility reducing compounds and toxins - Size and growth form of food items	- Seasonal shifts in diet (Bergerud, 1972; Gaare & Skogland, 1975; Heggeberget, Gaare & Ball, 2002) - Selection of reproductive plant organs (Cooper Wookey, 2003) - Different food intake rates for different plant growth forms (Trudell & White, 1981)

My thesis demonstrates that more attention should be paid to the aspects that constrain food intake by reindeer. I base my conclusion on the fact that nutrient quality per se seems to play a minor role for reindeer at intermediate levels of feeding habitat selection, a level at which reindeer rather seem to be constrained in its food intake by food availability and quantity. Sub-arctic alpine environments have relatively low productivity with low standing crops of potential food plants. In other words, food is sparse and reindeer need to spend relatively more time in searching for food than they would in more high-productive environments. In addition, most of the potential food items are close to the ground often intermingled with non-food plant tissues, which makes food ingestion (and possibly also digestion) more difficult. I further propose that reindeer might switch between energy maximising and time minimising strategies depending on season, or even within seasons. During warm summer days with predicted high insect harassment, reindeer has been observed to dramatically reduce their time spent feeding from approximately 50% to 30% (Gaare, Thomson & Kjos-Hanssen, 1975; White et al., 1981). With current knowledge about food intake rates in arctic and sub-arctic environments, it seems likely that reindeer during those days only feed for a time period sufficient enough to fulfil their daily minimum energy requirements. It might also be so that reindeer switch between different feeding habitats depending on whether they adopt an energy maximising or time minimising strategy as the choice of optimal foods for these two strategies may be different.

I further conclude that the large-scaled migratory patterns observed among wild reindeer/caribou populations may be explained by phenological differences along climatic gradients. It is also possible that regional movements and feeding area selection may be affected by predation and parasite avoidance (Fig. 2). Although nutrient quality per se may explain habitat selection at higher levels (migratory patterns and movements between feeding areas), my analyses shows that it can only do so if reindeer switch their food preferences in accordance with seasonal shifts in nutrient quality between different plant groups. That is, inter-specific differences in plant nutrient dynamics in combination with different geographical distribution patterns of functional plant groups could give rise to the observed spatial distribution patterns of reindeer, but not intra-specific differences in plant nutrient dynamics alone. This is an important aspect in reindeer summer feeding ecology that would need to be incorporated in current theoretical frameworks. It is thus possible that reindeer by changing its diet could benefit from higher food quality during the period middle of June to the end of July by moving from low to high altitude, and between areas with early and late snowmelt. However, further studies would be needed to disentangle other confounding factors that might be equally or more important such as risk of predation, insect harassment and digestibility-reducing compounds.

Management implications

Implications for reindeer management

This study shows that spatial heterogeneity at the landscape level can be important to large herbivores. Conservation of large continuous landscapes can therefore be an important management goal, as they provide a wide range of habitats necessary for animals such as reindeer that use large territories. Any modifications of the landscape pattern due to area demanding activities such as mineral extraction, water dams and ski-resort structures should be in accordance with the requirements of ongoing reindeer herding activities.

Such heterogeneous alpine landscapes give rise to complex snowmelt patterns that in turn create climatic gradients across small as well as large spatial levels. Results from this study show that the potential benefits from altitudinal migration early in the plant growing season, in order to have access to high quality food, are reduced by the end of July. At this time, reindeer (or part of the reindeer herd) should be allowed to move into other areas and search for alternative forage such as mushrooms in the nearby sub-alpine forests, as high quality forage is only to be found at extremely high elevations where food biomass is sparse and might not support large reindeer herds.

Depending on grazing intensity, reindeer are capable of transforming tundra plant communities from low productive heath communities to high productive grass communities (Olofsson et al., 2001). It is therefore possible that reindeer by being highly selective as shown in my thesis, and through intensive use of specific feeding habitats such as alpine meadows and grass heaths, are able to maintain their summer pastures as high productive plant communities with preferred plant species such as herbs and graminioids. Reindeer management would thus need to consider minimum and maximum levels of grazing intensities that would be in relation to the long-term maintenance of preferred feeding habitats.

Implications for nature conservation

My thesis shows that diverse plant communities are preferred feeding habitats of reindeer during the plant growing season, and that as much as one fourth of the two most preferred feeding habitats within the study area were situated in areas designated for nature conservation. Reindeer grazing and browsing affect plant population demography in alpine and tundra ecosystems by removing substantial amounts of biomass and reproductive organs (Cooper & Wookey, 2003; den Herder et al., 2004). Consequently, reindeer grazing has had local effects on plant species diversity in Fennoscandia (Austrheim & Eriksson, 2001; Moen & Danell, 2003).

The study area is known for its rich flora with many rare and threatened species that are of national and international interest. Maintenance of plant species diversity in these alpine and tundra ecosystems should therefore be strongly connected to the reindeer management in the area in order to adopt a sustained level of grazing intensity. However, most of the redlisted species observed in the study area are lime-favoured species that grow in rocky or other poorly vegetated environments (Gärdenfors, 2005). This study shows that these habitats are either avoided or little used by feeding reindeer. Low to moderate grazing levels are therefore not likely to be a threat to the survival of these redlisted species.

Contrary, although reindeer grazing/browsing hampers growth and survival of certain plant species (Olofsson, 2001), other plant species such as a few rare and threatened plant species (e.g., *Arenaria norvegica*, *Botrychium boreale*, *Braya linearis*, *Draba fladnizensis*, and *Euphrasia salisburgensis*) at sites with high regional species diversity might depend on a certain grazing intensity (Olofsson & Oksanen, 2005) or level of disturbance by reindeer trampling (Gärdenfors, 2005). At high grazing levels, however, reindeer might use less preferred habitats and thus affect the population dynamics of many of the redlisted species as well as other more common plant species. The small population sizes of endangered species also make them vulnerable to erratic events where even low to moderate grazing levels can be a problem.

Future research needs

Diet selection

Grazing in meadows with a mixture of graminioids and herbs, browsing of deciduous dwarf shrubs, and browsing of deciduous tall shrubs and trees are the dominant summer feeding modes of reindeer. Although elementary models of functional responses to predict food intake of summer forage has been developed for reindeer/caribou, these need to be further developed taking into account recent findings about the mechanisms behind food intake of deer. These models can then be valuable tools to be used to quantitatively test predictions of general foraging theory, as well as to precisely estimate carrying capacities of summer ranges. In addition, these models should consider the role of plant secondary compounds in the diet of reindeer/caribou, which so far has been very little studied. It is possible that plant secondary compounds can partly explain the seasonal shifts in diet observed among reindeer/caribou.

So far, most studies related to diet selection and feeding unit selection of reindeer have been observational studies. Experimental manipulations, for example cafeteria experiments (Danell et al., 1994) carried out in the field, could give new knowledge on the importance of forage quality and quantity. Specifically, through greenhouse experiments it would be possible to experimentally change the components of plant nutrient quality of reindeer forage species, that could then be transplanted to preferred feeding habitats during different parts of the season. Likewise, fertilisation trials (Ball,Danell & Sunesson, 2000) and snowmelt manipulations (Walsh et al., 1997) could be used in the field to create experimental study plots with different food quality. To extend the spatio-temporal model of plant nutrient dynamics to also include other important reindeer forage species and geographical areas would also provide a basis to quantitatively test the high-quality-food-seeking hypothesis as well as to develop optimal management strategies with regard to plant nutrient dynamics.

Community ecology

During spring, reindeer pass through the birch forest-alpine ecotone where they can exert a strong browsing pressure on mountain birch trees, saplings and seedlings. This browsing pressure has significant effect on the tree line dynamics in the Scandinavian mountains. To study the interactions in the system composed of mountain birch, defoliating insects and reindeer might give further insight in aspects of foraging ecology of reindeer, as well as tree line dynamics and the interactions between different guilds of herbivores.

References

Albon, S.D. & Langvatn, R. 1992. Plant phenology and the benefits of migration in a temperate ungulate. *Oikos 65*, 502-513.

Alexandersson, H., Karlström, C. & Larsson-McCann, S. 1991. Temperature and precipitation in Sweden 1961-90. Reference normals. *Meteorologi No. 81*, Norrköping, SMHI. (In Swedish with English summary.)

Andersen, J.R. & Nilsen, A.C. 1998. Do reindeer aggregate on snow patches to reduce harassment by parasitic flies or to thermoregulate? *Rangifer 18*, 1-15.

Andersson, N.Å., Callaghan, T.V. & Karlsson, P.S. 1996. The Abisko Scientific Research Station. *Ecological Bulletins 45*, 11-14.

Austrheim, G. & Eriksson, O. 2001. Plant species diversity and grazing in the Scandinavian mountains - patterns and processes at different scales. *Ecography 24*, 683-695.

Ball, J.P., Danell, K. & Sunesson, P. 2000. Response of a herbivore community to increased food quality and quantity: an experiment with nitrogen fertilizer in a boreal forest. *Journal of Applied Ecology 37*, 247-255.

Baskin, L.M. 1986. Differences in the ecology and behaviour of reindeer populations in the USSR. *Rangifer, Special Issue No. 1*, 333-340.

Baskin, L. & Danell, K. 2003. *Ecology of ungulates. A handbook of species in eastern Europe and northern and central Asia*. Springer-Verlag, Berlin.

Bell, R.H.V. 1970. *The use of the herb layer by grazing ungulates in the Serengeti*. In: Animal populations in relation to their food resources. (Ed. A. Watson). Blackwell Scientific Publications, New York, pp. 111-123.

Bell, W.J. 1990. *Searching behaviour. The behavioural ecology of finding resources*. Chapman and Hall, London.

Bergerud, A.T. 1972. Food habits of Newfoundland caribou. *Journal of Wildlife Management 36*, 913-923.

Bergerud, A.T. 1996. Evolving perspective on caribou population dynamics, have we got it right yet? *Rangifer Special Issue No. 9*, 95-115.

Bergerud, A.T., Butler, H.E. & Miller, D.R. 1984. Antipredator tactics of calving caribou: dispersion in mountains. *Canadian Journal of Zoology 62*, 1566-1575.

Bergerud, A.T. & Elliot, J.P. 1986. Dynamics of caribou and wolves in northern British Columbia. *Canadian Journal of Zoology 64*, 1515-1529.

Bergerud, A.T. & Page, R.E. 1987. Displacement and dispersion of parturient caribou at calving as antipredator tactics. *Canadian Journal of Zoology 65*, 1597-1606.

Berglund, B.E., Barnekow, L., Hammarlund, D., Sandgren, P & Snowball, I.F. 1996. Holocene forest dynamics and climate changes in the Abisko area, northern Sweden - the Sonesson model of vegetation history reconsidered and confirmed. *Ecological Bulletins 45*, 15-30.

Billings, W.D. & Bliss, L.C. 1959. An alpine snowbank environment and its effect on vegetation, plant development, and productivity. *Ecology 40*, 388-397.

Bryant, E.H. 1973. Habitat selection in a variable environment. *Journal of Theoretical Biology 41*, 421-429.

Bryant, J.P. & Kuropat, P.J. 1980. Selection of winter forage by subarctic browsing vertebrates: The role of plant chemistry. *Annual Reviews of Ecology and Systematics 11*, 261-285.

Chapin III, F.S., Johnson, D.A. & McKendrick, J.D. 1980. Seasonal movement of nutrients in plants of differing growth form in an Alaskan tundra ecosystem: implications for herbivory. *Journal of Ecology 68*, 189-209.

Chapin III, F.S., Van Cleve, K. & Tieszen, L.L. 1975. Seasonal nutrient dynamics of tundra vegetation at Barrow, Alaska. *Arctic and Alpine Research 7*, 209-226.

Charnov, E.L. 1976. Optimal foraging: The marginal value theorem. *Theoretical Population Biology 9*, 129-136.

Cooper, E.J. & Wookey, P.A. 2003. Floral herbivory of Dryas octopetala by Svalbard reindeer. *Arctic, Antarctic, and Alpine Research 35*, 369-376.

Cransac, N. & Hewison, A.J.M. 1997. Seasonal use and selection of habitat by mouflon (*Ovis gmelini*): Comparison of the sexes. *Behavioural Processes 41*, 57-67.

Dahle, H.K., Danell, Ö., Gaare, E. & Nieminen, M. (eds.) 1999. *Reindrift i Nordvest-Europa i 1998 - biologiske muligheter og begrensninger*. Nordisk Ministerråd (NMR), København.

Danell, K., Utsi, P.M., Palo, R.T. & Eriksson, O. 1994. Food plant selection by reindeer during winter in relation to plant quality. *Ecography 17*, 153-158.

Dearing, M. D., Mangione, A.M. & Karasov, W.H. 2000. Diet breadth of mammalian herbivores: nutrient versus detoxification constraints. *Oecologia 123*, 397-405.

Demment, M.W. & van Soest, P. 1985. A nutritional explanation for body-size patterns of ruminant and non-ruminant herbivores. *The American Naturalist 125*, 641-672.

den Herder, M., Virtanen, R. & Roininen, H. 2004. Effects of reindeer browsing on tundra willow and its associated insect herbivores. *Journal of Applied Ecology 41*, 870-879.

Downes, C.M., Theberge, J.B. & Smith, S.M. 1986. The influence of insects on the distribution, microhabitat choice, and behavior of the Burwash caribou herd. *Canadian Journal of Zoology 64*, 622-629.

Dumont, B., Carrère, P. & D'Hour, P. 2002. Foraging in patchy grasslands: diet selection by sheep and cattle is affected by the abundance and spatial distribution of preferred species. *Animal Research 51*, 367-381.

Edenius, L., Vencatasawmy, C.P., Sandström, P. & Dahlberg, U. 2003. Combining satellite imagery and ancillary data to map snowbed vegetation important to reindeer *Rangifer tarandus*. *Arctic, Antarctic, and Alpine Research 35*, 150-157.

Emlen, J. M. 1966. The role of time and energy in food preference. *The American Naturalist 100*, 611-617.

Fancy, S.G. & Whitten, K.R. 1991. Selection of calving sites by Porcupine herd caribou. *Canadian Journal of Zoology 69*, 1736-1743.

Ferguson, S.H. & Elkie, P.C. 2004. Seasonal movement patterns of woodland caribou (*Rangifer tarandus caribou*). *Journal of Zoology 262*, 125-134.

Festa-Bianchet, M. 1988. Seasonal range selection in bighorn sheep: conflicts between forage quality, forage quantity and predator avoidance. *Oecologia 75*, 580-586.

Focardi, S., Marcellini, P. & Montanaro, P. 1996. Do ungulates exhibit a food density threshold? A field study of optimal foraging and movement patterns. *Journal of Animal Ecology 65*, 606-620.

Folstad, I., Nilssen, A.C., Halvorsen, O. & Andersen, J. 1991. Parasite avoidance: the cause of post-calving migrations in Rangifer? *Canadian Journal of Zoology 69*, 2423-2429.

Freeland, W.J. & Janzen, D.H. 1974. Strategies in herbivory by mammals: the role of plant secondary compounds. *The American Naturalist 108*, 269-289.

Fretwell, S.D. 1972. *Populations in a seasonal environment*. Princeton University Press, Princeton, NJ.

Gaare, E. & Skogland, T. 1975. *Wild reindeer food habits and range use at Hardangervidda*. In: Fennoscandian tundra ecosystems. Part 2: Animals and systems analysis. (Ed. F.E. Wielgolaski). Springer-Verlag, Berlin, pp. 195-205.

Gaare, E., Thomson, B.R. & Kjos-Hanssen, O. 1975. *Reindeer activity on Hardangervidda.* In: Fennoscandian tundra ecosystems. Part 2. Animals and systems analysis. (Ed. F.E. Wielgolaski). Springer-Verlag, Berlin, pp. 206-215.

Gärdenfors, U. 2005. *Rödlistade arter i Sverige 2005. The 2005 redlist of Swedish species*. Artdatabanken, SLU, Uppsala, Sweden.

Gates, C.C., Adamczewski, J. & Mulders, R. 1986. Population dynamics, winter ecology and social organization of Coats Island caribou. *Arctic 39*, 216-222.

Gross, J.E., Shipley, L.A., Hobbs, N.T., Spalinger, D.E. & Wunder, B.A. 1993. Functional response of herbivores in food-concentrated patches: tests of a mechanistic model. *Ecology 74*, 778-791.

Hall, L.S., Krausman, P.R. & Morrison, M.L. 1997. The habitat concept and a plea for standard terminology. *Wildlife Society Bulletin 25*, 173-182.

Hanley, T.A. 1997. A nutritional view of understanding and complexity in the problem of diet selection by deer (Cervidae). *Oikos 79*, 209-218.

Hassell, M.P. & Southwood, T.R.E. 1978. Foraging strategies of insects. *Annual Review of Ecology and Systematics 9*, 75-98.

Heggberget, T.M., Gaare, E. & Ball, J.P. 2002. Reindeer (*Rangifer tarandus*) and climate change: Importance of winter forage. *Rangifer 22*, 75-94.

Hofmann, R.R. 1973. *The ruminant stomach: stomach structure and feeding habits of East African game ruminants*. East African Monographs in Biology 2, East African Literature Bureau, Nairobi.

Hofmann, R.R. 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comprehensive review of their digestive system. *Oecologia 78*, 443-457.

Hughes, J.J., Ward, D. & Perrin, M.R. 1994. Predation risk and competition affect habitat selection and activity of Namib desert gerbils. *Ecology 75*, 1397-1405.

Illius, A.W. & Gordon, I.J. 1990. *Constraints on diet selection and foraging behaviour in mammalian herbivores*. In: Diet selection - An interdisciplinary approach to foraging behaviour. (Ed. R.N. Hughes). Blackwell Scientific Publications, Oxford, pp. 157-181.

Ion, P.G. & Kershaw, G.P. 1989. The selection of snowpatches as relief habitat by woodland caribou (*Rangifer tarandus caribou*), Macmillan Pass, Selwyn/Mackenzie Mountains, N.W.T., Canada. *Arctic and Alpine Research 21*, 203-211.

Jarman, P.J. 1974. The social organisation of antelope in relation to their ecology. *Behaviour 48*, 215-267.

Johnson, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology 61*, 65-71.

Kareiva, P.M. & Shigesada, N. 1983. Analyzing insect movement as a correlated random walk. *Oecologia 56*, 234-238.

Klein, D.R. 1970. Tundra ranges north of the boreal forest. *Journal of Range Management 23*, 8-14.

Klein, D.R. 1990. Variation in quality of caribou and reindeer forage plants associated with season, plant part, and phenology. *Rangifer, Special Issue No. 3*, 123-130.

Klein, D.R. 1996. Arctic ungulates at the northern edge of terrestrial life. *Rangifer 16*, 51-56.

Klein, D.R. & Bay, C. 1994. Resource partitioning by mammalian herbivores in the high Arctic. *Oecologia 97*, 439-450.

Körner, C. 1989. The nutritional status of plants from high altitudes. *Oecologia 81*, 379-391.

Körner, C. 1999. *Alpine plant life: Functional plant ecology of high mountain ecosystems*. Springer-Verlag, Heidelberg.

Kudo, G., Nordenhäll, U. & Molau, U. 1999. Effects of snowmelt timing on leaf traits, leaf production, and shoot growth of alpine plants: Comparisons along a snowmelt gradient in northern Sweden. *Ecoscience 6*, 439-450.

Langvatn, R., Albon, S.D., Burkey, T. & Clutton-Brock, T.H. 1996. Climate, plant phenology and variation in age of first reproduction in a temperate herbivore. *Journal of Animal Ecology 65*, 653-670.

Leader-Williams, N., Scott, T.A. & Pratt, R.M. 1981. Forage selection by introduced reindeer on South Georgia, and its consequences for the flora. *Journal of Applied Ecology 18*, 83-106.

Levin, S.A. 1992. The problem of pattern and scale in ecology. *Ecology 73*, 1943-1967.

Lima, S.L. & Dill, L.M. 1990. Behavioural decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology 68*, 619-640.

Lönnberg, E. 1909. *Renarne och deras lefnadsvanor*. Uppsala, Sweden.

Manker, E. 1953. The nomadism of the Swedish mountain lapps: their siidas and their migratory routes in 1945. *Acta Lapponica 7*, 1-261.

MacArthur, R.H. & Pianka, E.R. 1966. On optimal use of a patchy environment. *The American Naturalist 100*, 603-609.

Manly, B.F.J., McDonald, L.L. & Thomas, D.L. 1993. *Resource selection by animals: statistical design and analysis for field studies*. Chapman & Hall, London.

Mauritzen, M., Belikov, S.E., Boltunov, A.N., Derocher, A.E., Hansen, E., Ims, R.A., Wiig, Ø. & Yoccoz, N. 2003. Functional responses in polar bear habitat selection. *Oikos 100*, 112-124.

McNaughton, S.J. 1990. Mineral nutrition and seasonal movements of African migratory ungulates. *Nature 345*, 613-615.

Mengel, K. & Kirkby, E.A. 1987. *Principles of plant nutrition*. International Potash Institute, Bern.

Moen, J. & Danell, Ö. 2003. Reindeer in the Swedish mountains: An assessment of grazing impacts. *Ambio 32*, 397-402.

Nellemann, C. & Cameron, R.D. 1996. Effects of petroleum development on terrain preferences of calving caribou. *Arctic 49*, 23-28.

Nellemann, C. & Thomsen, M.G. 1994. Terrain ruggedness and caribou forage availability during snowmelt on the Arctic Coastal Plain, Alaska. *Arctic 47*, 361-367.

Nieminen, M. & Heiskari, U. 1989. Diets of freely grazing and captive reindeer during summer and winter. *Rangifer 9*, 17-34.

Niia, L.P. 1986. Renskötsel och kommunal planering. [Reindeer husbandry and local planning.] *Rangifer 6*, 36-43.

Nordengren, C. & Ball, J.P. 2005. A field assessment of the Spalinger-Hobbs mechanistic foraging model: free-ranging moose in winter. *Canadian Journal of Zoology 83*, 518-526.

Olofsson, J. 2001. Influence of herbivory and abiotic factors on the distribution of tall forbs along a productivity gradient: a transplantation experiment. *Oikos 94*, 351-357.

Olofsson, J., Kitti, H., Rautiainen, P., Stark, S. & Oksanen, L. 2001. Effects of summer grazing by reindeer on composition of vegetation, productivity and nitrogen cycling. *Ecography 24*, 13-24.

Olofsson, J. & Oksanen, L. 2005. Effects of reindeer density on vascular plant diversity on North Scandinavian mountains. *Rangifer 25*, 5-18.

Orians, G.H. & Wittenberger, J.F. 1991. Spatial and temporal scales in habitat selection. *The American Naturalist 137*, 29-49.

Parker, G.A. & Maynard Smith, J. 1990. Optimality theory in evolutionary biology. *Nature 348*, 27-33.

Pastor, J., Standke, K., Farnsworth, K., Moen, R., & Cohen, Y. 1999. Further development of the Spalinger-Hobbs mechanistic foraging model for free-ranging moose. *Canadian Journal of Zoology 77*, 1505-1512.

Perry, G. & Pianka, E.R. 1997. Animal foraging: past, present and future. *Trends in Ecology and Evolution 12*, 360-364.

Post, E.S. & Klein, D.R. 1996. Relationships between graminoid growth form and levels of grazing by caribou (*Rangifer tarandus*) in Alaska. *Oecologia 107*, 364-372.

Post, E. & Klein, D.R. 1999. Caribou calf production and seasonal range quality during a population decline. *Journal of Wildlife Management 63*, 335-345.

Post, E. & Stenseth, N.C. 1999. Climatic variability, plant phenology, and northern ungulates. *Ecology 80*, 1322-1339.

Provenza, F.D., Villalba, J.J., Dziba, L.E., Atwood, S.B. & Banner, R.E. 2003. Linking herbivore experience, varied diets, and plant biochemical diversity. *Small Ruminant Research 49*, 257-274.

Pyke, G.H., Pulliam, H.R. & Charnov, E.L. 1977. Optimal foraging: a selective review of theory and tests. *The Quarterly Review of Biology 52*, 137-154.

Riipi, M., Haukioja, E., Lempa, K., Ossipov, V., Ossipova, S. & Pihlaja, K. 2004. Ranking of individual mountain birch trees in terms of leaf chemistry: seasonal and annual variation. *Chemoecology 14*, 31-43.

Robbins, C.T. 1993. *Wildlife feeding and nutrition*. Academic Press Inc., San Diego.

Røed, K.H. 2005. Refugial origin and postglacial colonization of holarctic reindeer and caribou. *Rangifer 25*, 19-30.

Sandström, P., Granqvist Pahlén, T., Edenius, L., Tømmervik, H., Hagner, O., Hemberg, L., Olsson, H., Baer, K., Stenlund, T., Brandt, L.G. & Egberth, M. 2003. Conflict resolution by participatory management: Remote sensing and GIS as tools for communicating land-use needs for reindeer herding in northern Sweden. *Ambio 32*, 557-567.

Schaefer, J.A. & Messier, F. 1995. Scale-dependent correlations of Arctic vegetation and snow-cover. *Arctic and Alpine Research 27*, 38-43.

Schoener, T.W. 1971. Theory of feeding strategies. *Annual Review of Ecology and Systematics 2*, 369-404.

Senft, R.L., Coughenour, M.B., Bailey, D.W., Rittenhouse, L.R., Sala, O.E. & Swift, D.M. 1987. Large herbivore foraging and ecological hierarchies. *BioScience, 37*, 789-799.

Sjörs, H. 1999. The background: geology, climate and zonation. *Acta Phytogeographica Suecica 84*, 5-14.

Skjenneberg, S. & Slagsvold, L. 1968. *Rein driften og dens naturgrunnlag*. Universitetsforlaget, Oslo, Norway.

Skogland, T. 1980. Comparative summer feeding strategies of arctic and alpine *Rangifer*. *Journal of Animal Ecology 49*, 81-98.

Skogland, T. 1984. Wild reindeer foraging-nich organization. *Holarctic Ecology 7*, 345-379.

Skogland, T. 1989. Comparative social organization of wild reindeer in relation to food, mates and predator avoidance. *Advances in Ethology 29*, 1-74.

Spalinger, D.E. & Hobbs, N.T. 1992. Mechanisms of foraging in mammalian herbivores: new models of functional response. *The American Naturalist 140*, 325-348.

Spitz, F. & Janeau, G. 1995. Daily selection of habitat in wild boar (*Sus scrofa*). *Journal of Zoology, London, 237*, 423-434.

Staaland, H., Scheie, J.O., Grøndahl, F.A., Persen, E., Leifseth, A.B. & Holand, Ø. 1993. The introduction of reindeer to Brøggerhalvøya, Svalbard: grazing and effect on vegetation. *Rangifer 13*, 15-19.

Stephens, D.W. & Krebs, J.R. 1986. *Foraging theory*. Princeton University Presss, Princeton, New Jersey.

Toupin, B., Huot, J. & Manseau, M. 1996. Effect of insect harassment on the behaviour of the Rivière George caribou. *Arctic 49*, 375-382.

Trudell, J. & White, R.G. 1981. The effect of forage structure and availability on food intake, biting rate, bite size and daily eating time of reindeer. *Journal of Applied Ecology 18*, 63-81.

Turchin, P. 1996. Fractal analyses of animal movement: a critique. *Ecology 77*, 2086-2090.

Tveraa, T., Fauchald, P., Henaug, C. & Yoccoz, N.G. 2003. An examination of a compensatory relationship between food limitation and predation in semi-domestic reindeer. *Oecologia 127*, 370-376.

van der Wal, R., Madan, N., van Lieshout, S., Dormann, C., Langvatn, R. & Albon, S.D. 2000. Trading forage quality for quantity? Plant phenology and patch choice by Svalbard reindeer. *Oecologia 123*, 108-115.

van Wijk, M.T., Williams, M., Laundre, J.A. & Shaver, G.R. 2003. Interannual variability of plant phenology in tussock tundra: Modelling interactions of plant productivity, plant phenology, snowmelt and soil thaw. *Global Change Biology 9*, 743-758.

Viswanathan, G.M., Buldyrev, S.V., Havlin, S., da Luz, M.G.E., Raposo, E.P. & Stanley, H.E. 1999. Optimizing the success of random searches. *Nature 401*, 911-914.

Walsh, N.E., Fancy, S.G., McCabe, T.R. & Pank, L.F. 1992. Habitat use by the Porcupine caribou herd during predicted insect harassment. *Journal of Wildlife Management 56*, 465-473.

Ward, D. & Saltz, D. 1994. Foraging at different spatial scales: Dorcas gazelles foraging for lilies in the Negev desert. *Ecology 75*, 48-58.

White, R.G. 1983. Foraging patterns and their multiplier effects on productivity of northern ungulates. *Oikos 40*, 377-384.

White, R.G., Bunnell, F.L., Gaare, E., Skogland, T. & Hubert, B. 1981. *Ungulates on arctic ranges*. In: Tundra ecosystems: a comparative analysis. (Eds. L.C. Bliss, O.W. Heal & J.J. Moore). Cambridge University Press, Cambridge, pp. 397-483.

Whitten, K.R. & Cameron, R.D. 1980. *Nutrient dynamics of caribou forage on Alaska's north slope*. In: Proceeding of the Second International Reindeer/Caribou Symposium 17-21 September 1979, Røros, Norway. (Eds. E. Reimers, E. Gaare & S. Skjenneberg). Direktoratet for vilt og ferskvannsfisk, Trondheim, pp.159-166.

Wickstrom, M.L., Robbins, C.T., Hanley, T.A., Spalinger, D.E. & Parish, S.M. 1984. Food intake and foraging energetics of elk and mule deer. *Journal of Wildlife Management 48*, 1285-1301.

Wiens, J.A. 1976. Population responses to patchy environments. *Annual Review of Ecology and Systematics 7*, 81-210.

Williams, T.M. & Heard, D.C. 1986. World status of wild *Rangifer tarandus* populations. *Rangifer, Special Issue No. 1*, 19-28.

Wilmshurst, J.F. & Fryxell, J.M. 1995. Patch selection by red deer in relation to energy and protein intake: a re-evaluation of Langvatn and Hanley's (1993) results. *Oecologia 104*, 297-300.

Wilmshurst, J.F., Fryxell, J.M., Farm, B.P., Sinclair, A.R.E. & Henschel, C.P. 1999. Spatial distribution of Serengeti wildebeest in relation to resources. *Canadian Journal of Zoology 77*, 1223-1232.

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