Morphological and Behavioural Adaptations of Moose to Climate, Snow, and Forage

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Abstract

This thesis focuses on the behavioural and morphological adaptations of moose to snow and climate: specifically, seasonal migration, habitat choice, and following behaviour, plus the relationships among morphology, climate, snow, and seasonality. I examine intake and availability of winter forage, and perform one of the first large-scale tests of a widely used optimal foraging model by videotaping free-ranging moose making their own choices. The study of seasonal migration and habitat choice showed that the effect of snow differs with variation in snow severity: in locations with large differences in snow depths in a short distance, snow depth is important, but in locations where snow depth is less variable, snow quality emerges as more important. The thesis is one of the first to use a new method to evaluate the importance of snow quality. Testing between competing hypotheses to explain morphology, the importance of snow was further emphasized relative to temperature and latitude. In snowier areas, moose had larger hooves and longer legs than expected from their size and age. Morphology both conformed to, and was in opposition to some of the most well-known ecogeographical rules: in areas with cold winters, moose were heavier (Bergmann's rule) and had shorter ears (Allen's rule). There was also some evidence that moose morphology was related to heat stress during summer. The quality of the two main winter forages (birch and willows) differed within and between species. Willows had more available browse, and lower levels of secondary defence compounds than birch, but also less nitrogen and more fibre. These differences in forage quality also emerged in the test of the Spalinger-Hobbs model, as moose preferentially fed on willow, which was also the faster food to ingest. Most importantly, the analysis revealed that the foraging parameters varied within a foraging bout, and thus parameterizing the model from only the first few minutes of a bout would greatly mis-estimate intake. In the face of climate change, my results emphasize the need for research relating behaviour and morphology to environmental conditions. As moose are well adapted to snow and winter conditions, climate change may have negative consequences on southern populations as temperatures will rise, and some ranges may become unsuitable.

Keywords: moose, adaptations, behavior, morphology, winter, climate, snow, forage, optimal foraging.

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“First, therefore I will speak of the Elke, which the Savages call a Mose: it is a very large Deare, with a very faire head, and a broad palme, like the palme of a fallow Deares horne, but much bigger, and is 6 footewide between the tipps, which grow curbing downwards: he is of the bignesse of a great horse”.

Samuel Champlain, 1603

Contents

List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Ball, John P., Nordengren, C. and Wallin, K. (2001). Partial migration by large ungulates: Characteristics of seasonal moose ranges in northern Sweden. *Wildlife Biology* 7(1), 39-47.

II Lundmark, C. and Ball, John P. (2008). Living in Snowy Environments: Quantifying the Influence of Snow on Moose Behavior. *Arctic, Antarctic, and Alpine Research* 40(1), 111-118.

III Ball, John P., Lundmark, C., Ericsson, G., Wallin, K. and Danell, K. Bergmann's rule, Allen's rule, and snow: Testing hypotheses of geographic variation in moose morphology. *Manuscript.*

IV Nordengren, C., Hofgaard, A.and Ball, John P. (2003). Availability and quality of herbivore winter browse in relation to tree height and snow depth. *Annales Zoologici Fennici* 40 (3), 305-314.

V Nordengren, C. and Ball, John P. (2005). A field assessment of the Spalinger-Hobbs mechanistic foraging model: Free-ranging moose in winter. *Canadian Journal of Zoology* 83 (4), 518-526.

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Introduction

Ungulates and their environment

One of the central concerns of wildlife ecology is to understand the interactions between the animals and their environments. For ungulates, both survival and distribution are dependent on abiotic as well as biotic factors, including availability and quality of forage, as well as climate conditions and competition for resources. At high latitudes, ungulates are exposed to a great annual range of climatic conditions. This strongly seasonal climate results in long and cold winters with reduced forage availability, followed by short and intense summers with prolonged daylight, high temperatures and an intense burst of available food of high quality. Understanding how animals survive and thrive in these areas has long been a challenge to ecologists, and has led to the development of several theories and hypotheses to explain the relationships among climate and the behaviour and morphology of animals.

In seasonal ecosystems, winter is often the critical time of the year, and the occurrence of snow, cold, and the costs of gaining and allocating energy has shaped many of the evolutionary responses of ungulates inhabiting these areas (Halfpenny and Ozanne, 1989; Parker and Gillingham, 1990). During winter, low ambient temperatures affects metabolic rates and induces biochemical changes (Schwartz et al., 1988; Halfpenny and Ozanne, 1989; Parker *et al*, 1993), there is no increment in food resources, snow covers much of the food and increases the energy cost for locomotion (Coady, 1974; Sandegren *et al.*, 1985; Klein, 1995). When mobility is restricted and food resources are limited due to snow, survival is often strongly affected by heat and energy conservation.

In my thesis, I mainly focus on the behavioural and morphological adaptations of moose to climate conditions, and examine intake and forage that is available to moose during winter.

The moose (*Alces alces*) is the largest member of the deer family, and can reach a live weight of 650 kg or more, males being generally larger than females. The European moose evolved in Eurasia some 100 000 – 300 000 years ago (Bubenik, 1998), and the first moose arrived in Scandinavia following the receding ice after the latest glaciation 9000 – 10 000 BP (Cederlund and Bergström, 1996). The size and distribution of the Swedish moose population has varied dramatically: in the beginning of the 19th century, moose numbers reached a record-low with only small populations left in mid-Sweden (Bergström et al., 1993; Åkerberg, 2005). After changes in harvest strategies together with a reduction of the Scandinavian carnivore populations, the population started to recover. Subsequent changes in forest practices in the 1960's and 1970's allowed the moose population to increase further until it reached a (post-harvest) population size of approximately 315 000 individuals in the early 1980's (Hörnberg, 1991; Ingemarson, 2005). Today, the post-harvest population size is approximately 200 000 individuals (Kindberg *et al.*, 2008). Consequently, harvest numbers have changed as well, and peaked in the beginning of the 1980's, when almost 175 000 moose were harvested annually (Bergström et al., 1993), compared to 82 370 individuals in 2007 (Kindberg *et al.*, 2008). The economic significance of the moose population is substantial, with an annual hunting value close to 1.43 billion SEK, incorporating recreational as well as meat values (Mattsson et al, 2007). There are, however, also several negative aspects of the moose population. Moose-vehicle accidents now number almost 5000 accidents annually, with a cost of almost 340 million SEK (Swedish Road Administration), and the severe browsing damage caused by moose on young forest stands (Persson et al, 2000; Lavsund, 2003), results in annual costs of up to 1.30 billion SEK (Glöde *et al.*, 2004).

The moose is classified as a concentrate selector (Hofmann, 1985), and meets its nutritional requirements by consuming a wide variety of plants and plant parts. Generally, moose prefer deciduous species, dwarf shrubs, and herbs such as rowan *Sorbus aucuparia* L. willow *Salix* spp., aspen *Populus tremuloides* L., birch *Betula pendula* L. and *B. pubescens* L., oak *Quercus robur* L., blueberrry *Vaccinum myrtillus* L., meadowsweet *Filipendula ulmaria*, L., grasses Poaceae spp. and sedges *Carex* spp. (Bergström and Hjeljord, 1987; Shipley et al., 1998, Broman, 2003;

Månsson *et al.*, 2007). During winter, the selection of available browse is scarce, and mainly consist of annual shoots of deciduous trees such as willow and birch, and annual shoots of pine *Pinus sylvestris* L. (Shipley et al, 1998). To fulfil its nutritional requirements during winter, the moose has to consume 3-6 kg twigs (dry weight) daily (Baskin and Danell, 2003).

In this thesis, the moose was chosen as the main study object, since its distribution covers almost the entire range of Sweden, ranging from the coastal areas in the south-east, to the mountain ranges in the north-west. The moose is well adapted to a variety of different habitats and environmental conditions, and well suited for a life in the cold. The moose is thus a suitable object when studying morphology, behaviour, and foraging topics, especially with regard to various climate regimes, and to provide insight into how this important ungulate's morphology may change under climate change.

Behavioural and morphological adaptations to life at high latitudes

"If an animal didn't need legs for mobility, it would be far better off without them" Halfpenny and Ozanne, 1989

Ungulates at high latitude areas have evolved numerous adaptations that enable them to survive in their periodically harsh environments. Some of these adaptations relate to morphology and physiology, and include features such as long legs that allow easy movement through deep snow (Bubenik, 1998), large hooves with tendons and cartilage that allow the digits and dewclaws to spread on soft surfaces and to squeeze together before lifting the hoof (Coady, 1974), and an exceptionally isolative winter hair coat (Geist, 1987). Physiological adaptations also include nasal and counter-current heat exchange to reduce heat loss (Marchand, 1991), and changes in activity levels and metabolic rate (Parker and Robbins, 1984; Renecker and Hudson, 1986; Cederlund et al, 1989; Parker *et al.*, 1993).

As a consequence of being so well-adapted to cold, many northern ungulates are easily heat stressed during both summer and winter, which may lead to a decline in their physical condition (Parker and Robbins 1984; Renecker and Hudson 1986; Sargeant *et al.*, 1994). The moose is an excellent example of a cold-tolerant species, as their large body size, long legs, and warm pelage makes them extremely well adapted to winter conditions (Renecker and Hudson, 1986; Dussault *et al.*, 2004). Of the northern ungulates, moose are perhaps the best adapted to cold temperatures: the lower extreme of the thermal-neutral zone (below which moose must expend energy to maintain body heat) lies somewhere below -30C for winter-adapted moose (Renecker and Hudson, 1986). Instead, moose instead have great difficulty in dissipating surplus heat during warm temperatures, particularly during late winter and spring (Parker and Robbins, 1984; Renecker and Hudson, 1986; Dussault *et al.*, 2004) when temperatures above -5°C may cause heat stress (Renecker and Hudson, 1986). However, the long legs of moose might be important in thermoregulation by allowing them to radiate excess heat (Kelsall and Telfer, 1974) and thus may help to reduce heat stress. For moose, it has been suggested that its distribution is limited by warm rather than cold temperatures (Renecker and Hudson, 1986; Karns, 1998; Van Ballenberghe and Ballard, 1998).

In addition to morphological and physiological adaptations, the survival of most over-wintering animals is dependent on their actions. High latitude ungulates like the moose are known to adjust their behaviour according to environmental properties at both large (migration between seasonal ranges) and small (within over-wintering ranges) scales (Coady, 1974; Telfer and Kelsall, 1984; Ballard et al., 1991; Nicholson et al., 1997; Bruggeman *et al.*, 2006). Migration is a common behaviour of herbivores at high latitudes, and involves trade-offs in the allocations of time and energy, especially when considering the travel costs between ranges. Understanding migration and habitat selection within home ranges may therefore involve foraging conditions and models based on optimal foraging theory (Börger *et al.*, 2008). When considering the importance of the vegetation, migration patterns of ungulates has been suggested to be influenced by the tendency for the animals to utilize food plants that may differ in importance during different seasons and/or grow in different habitats (Thompson and Vukelich, 1981; Bergström and Hjeljord, 1987). Migration has also been suggested to be determined by selection for high forage quality (*i.e.* the forage maturation hypothesis), and predicts that ungulates select for intermediate forage biomass to maximize energy intake by following phenological gradients while migrating (Hebblewhite *et al.*, 2008).

The distance between the summer and winter ranges of migrant moose varies considerably: some moose migrate 170 km, while others travel only very short distances (Ballard *et al.*, 1991) but still show a clear shift between non-overlapping ranges. The proportion of migrating animals increases towards the north, and may vary within a population due to changes in habitat suitability and climate severity (Ballard *et al.*, 1991; Dingle, 1996). Many studies suggest that moose migrate to winter areas with less snow and more suitable forage conditions (Coady 1974; Sweanor and Sandegren, 1989). In Scandinavia, moose populations below 60°N are not known to be migratory. With regard to snow conditions, not only snow depth, but also snow quality (*i.e.* density and hardness) may be important for migration and habitat choice, and snow quality has been shown to explain almost 90% of the variance in sinking depths (and hence the energetic cost of walking) of over-wintering ungulates (Bunnell *et al.*, 1990).

Since seasonal migration of northern ungulates still leaves them in snowy environments during winter, winter condition and survival can depend on them being able to reduce their energetic costs as much as possible even at smaller scales (*i.e.* within their winter ranges). One of the possible ways to do so is when the animal reduces the cost of walking in snow by placing its feet in the footprints of another animal (Fancy and White; 1985; Murray and Boutin, 1991; Crête and Larivière; 2003). This trail-following behaviour can reduce the energy spent when walking with more than half for the animal following behind (Fancy and White, 1985) – which can be of great importance for survival during winter. Moose are also able to use a special gait in deep snow (Figure 1), owing to the exceptional angle between the unusually long shin bone (tibia) and the metatarsus of the hind leg (Bubenik, 1998).

Figure 1. Moose walking in deep snow. Note the special gait used by moose. Photo: Eric Andersson.

"The moose is singularly grotesque and awkward to look at. Why should it stand so high at the shoulders? Why have so long a nose? Why have no tail to speak of?

Henry David Thoreau, 1817-1862

The geographical pattern in the morphology of mammals has long been of great interest to ecologists, and has lead to the development of numerous hypotheses relating morphology to the environment. Mammals in general show a pattern of being larger (*e.g.* Bergmann's rule, Bergmann, in Mayr, 1963), and having relatively shorter appendages (legs, ears, rostrum, etc) in the cooler parts of a species range (*e.g.* Allen's rule, Mayr, 1963). If animals in cold and snow-free areas are optimally designed according to the above rules, they should be large and have short thick legs in order to conserve heat. If however, snow rather than temperature acts as a selective force regarding foot size and leg length, feet should be larger and weight load (body weight/foot or hoof area) lighter to reduce the energetic cost of walking during winter (Parker *et al.*, 1984; Telfer and Kelsall, 1984; Fancy and White, 1985). Leg length also appears to be affected by several factors, such as nutritional constraints, heat conservation, efficiency of locomotion, and the ability to handle snow and to reach food (Coady, 1974; Parker *et al.*, 1984; Telfer and Kellsall, 1984; Fancy and White, 1985, Klein *et al.*, 1987; Murray and Boutin, 1991; Bubenik, 1998; Murray and Lariviére, 2002). There may thus be several, sometimes contradictory, selective forces acting on animal morphology, and the environmental causes for many of the observed morphological clines remains a subject of debate, and calls for further investigation.

So far, two often cited hypotheses (ecogeographical rules) have been proposed to explain the relationships between geography and size: Bergmann's rule (Bergmann 1847, in Mayr, 1963) hypothesised a general negative association between body size and environmental temperature, so that within a species, larger animals should be found in cooler climates or at higher latitudes. Allen's rule (Mayr, 1963) suggests that populations of the same species at higher latitudes tend to have shorter body appendages than population at lower latitudes, as the less surface area an organism has relative to its body mass, the less heat it will loose. Other hypotheses allied with the two above are James' hypothesis (James, 1970), and the size-dependent hypothesis (Olalla-Tárraga *et al.*, 2007), and other rather closely associated hypotheses that relate body sizes of mammals to productivity and/or seasonality (Boyce, 1978; Geist, 1987). Others yet relate body size to forage quality in seasonally variable environments (Jarman, 1974), release from competition (McNab, 1971), and habitat structure (Bro-Jørgensen, 2008).

To understand the morphological variations and adaptations of animals, it is important to include the climate variables influencing them. At high latitudes, the strong seasonality in weather conditions and in the availability and quality of forage poses especially strong selective pressure compared to areas where environmental conditions are more or less equal throughout the year (Boyce, 1978; Bradshaw and Holzapfel, 2008). The winter-adapted northern animals must thus be adapted both to cold temperatures and snow during winter, and to warm summers. Understanding the relationships between animal morphology and environmental conditions is now becoming increasingly important, given the predicted changes in climate Hofgaard *et al.*, 1999; Hughes, 2000; Millien *et al.*, 2006). Global warming is likely to affect both plants and animals, and poleward range expansions (and contractions for northern winter-adapted species) as well as morphological changes have already been indicated for several species (Hughes, 2000; Yom-Tov, 2001).

Foraging during winter

In boreal forests, ungulates such as the moose are not only consumers, but also have considerable impacts on their environment by modifying the structure and composition of their food plants (Persson et al., 2000; Stolter, 2008), and the energy balance and nutrient cycling within their habitats (Pastor and Cohen, 1997).

Forage intake of herbivores to a large extent depends on intrinsic constraints (*e.g.* morphological and physiological characteristics) which determines the range of foods they tolerate, and environmental constraints (such as seasonality) which affects the availability and quality of resources. The quality and quantity of forage is important for herbivores and strongly affects their feeding patterns within landscapes, as well as among browse species and individual plants and plant parts (Palo *et al.*, 1992; Hódar and Palo, 1997; Shipley *et al.*, 1998; Bergman *et al.*, 2001; Alm *et al.*, 2002; Behmer, 2002; Stolter *et al.*, 2005; Månsson *et al.*, 2007).

During winter, the reduction in available forage caused by snow accumulation and the subsequent decrease in food intake is potentially one of the most important mechanisms affecting animals during the winter (Hovey and Harestad, 1992; Klein, 1995; Loison *et al.*, 1999). One of the critical aspects of snow accumulation is how it reduces accessibility of forage at lower levels, but if the snow supports the weight of the herbivores, it also allows them to reach browse higher up a tree and previously out of reach. Variations in forage quantity and quality with height within a tree may thus be particularly important during the winter season, due to the changes in forage availability caused by snow. The digestive system of the ruminant moose is well adapted to process the woody winter browse efficiently: large bites and lengthy chewing breaks down the food material into particles capable of passing quickly out of the rumen, and as a generalist browser and concentrate selector (Belovsky, 1986) moose are also able to ingest moderate amounts of a variety of secondary plant compounds (Stolter *et al.*, 2005). In conformity with general optimal foraging theories, herbivores consume more slowly digestible forage in relation to its availability in times of low food abundance (*i.e.* during winter), as they become less selective when food abundance decreases (Owen-Smith and Novellie, 1982; Storms *et al.*, 2008). The moose thus appears to be a “nutrient mixer” during summer, and an “energy maximiser” during winter (Broman, 2003).

The demands on feeding ungulates during the critical time of year when they are forced to feed on low quality forage makes the winter season especially suitable for testing foraging theories. Constraints such as availability and quality of forage are crucial to foraging models, and have frequently been used to model forage intake of large ungulates (Belovsky 1978, Pyke, 1984; Illius and Gordon, 1991). In general, foraging theory predicts that herbivores will balance their diet as a result of nutritional needs, food quality, and availability of alternate foods, and aim at predicting forage intake with respect to time and energy spent, *vs.* energy gained while feeding. Most herbivore foraging models assume that intake rate is limited by the morphological and physiological abilities of consumption and processing, and thus focus on the constraints of searching, bite size, biting, and chewing (Shipley and Spalinger, 1992; Spalinger and Hobbs 1992; Gross *et al.*, 1993; Laca *et al.*, 1994; Woodward 1997). However, in most ungulate studies, measurements to parameterize these models have been confined to short term trials, using only a few minutes at the beginning of a bout of a captive, food-deprived ungulate, which seems a remarkably short duration for larger herbivores which may have foraging bouts exceeding an hour (Risenhoover, 1986; Cederlund *et al.*, 1989; Gillingham and Klein, 1991). If the assumptions regarding invariance throughout the longer foraging bouts of larger animals are perfectly met, the use of short term studies to parameterize the variables poses no risk. Conversely, if the parameters change during a bout, the estimated intake rate will be increasingly in error as the difference between the observation period (from which we extrapolate the parameter values) and the actual foraging bout increases. Therefore, employing foraging models (parameterised from short-term studies) on herbivores with long foraging bouts might be leading to mis-estimations of intake rates. Studies of large ungulates at a more realistic time scale are rare, and so far are limited to one study of two male moose, feeding on a single forage species in a large exclosure (Pastor *et al.*, 1999). One of the aims of this part of the thesis work was thus to study complete foraging bouts of wild, free-ranging moose making their own choices, in order to better test the Spalinger-Hobbs (1992) foraging model, and investigate the quantity, quality, and availability of winter forage.

Objectives

In this thesis, the main objectives were to study moose inhabiting high latitude areas to gain insight into their specific needs and adaptations in relation to winter conditions. Below, I list the main questions that were addressed in papers I – V. With an eye to the future, I also discuss the results from a climate change perspective.

1. How does large scale moose behaviour (*i.e.* seasonal migration) relate to environmental factors such as snow conditions and forage composition?

2. Do moose adjust their small-scale behaviour (*i.e.* within seasonal ranges) according to variations in quantity and quality of snow, and is there an easier way than those used today to quantify snow quality directly in the field?

3. If there is local adaptation in moose morphology to climate, is it a result of adaptation to cold winters, warm summers, or snow conditions?

4. How is forage availability affected by changing snow depths, and how does quantity and quality of forage vary within trees, as well as between climatologically different areas?

5. Does foraging moose in winter behave according to the assumptions of invariance with time made by most existing foraging models? Will the models need modifications when applied to wild ranging animals, or do we need to parameterize them differently than with values from short-term estimates of captive food-deprived animals?

Study area

The different studies of the thesis were performed in 21 locations spanning almost the entire length and breadth of Sweden (Figure 2).

The main part of the study (Papers II, IV, V, and parts of paper III) was performed close to Abisko (68°21′N, 18°49′E) in the mountains of northern Sweden. For paper IV, three separate locations were used ranging from the mountains of Abisko in the east, to the Norwegian coast 66 km to the west (grey colour on in Figure 2). Together, these locations form a steep climatic gradient with large differences in temperature and precipitation (Alexandersson *et al.*, 1991; Aune, 1993; Bjørbæck, 1993; Forland, 1993, Table 1). The study of migration and habitat choice in Paper I was conducted in the Robertsfors location just north of Umeå (black square in Figure 2). Moose morphology (Paper III) was studied in 19 of the 21 locations, spanning a 1245 km north-south gradient within Sweden, including locations from the Bothnian coast in the east, to the mountain range 483 km to the west.

The climate changes from south to north and from east to west with increasing winter severity and lower temperatures, and covers all vegetation zones in Sweden (Table 1). In the alpine vegetation zones, forested valleys are dominated by mountain birch, *Betula pubescens* ssp. Czerepanovii (Orlova) Hämet-Ahti in dry to mesic areas, and willows, *Salix* spp. in more moist areas. Additionally, aspen, *Populus tremula*, rowan, *Sorbus aucuparia*, and Scots pine, *Pinus sylvestris* occur as scattered individuals or stands. The treeline is 700–800 m a.s.l., with surrounding mountains within the study locations reaching up to 1700 m a.s.l. During the growing season, the area is used as grazing grounds for reindeer *Rangifer tarandus*. In the boreal zones, the forests are dominated by Scots pine *Pinus sylvestris*, and Norway spruce *Pícea abies,* interspersed with birch, *Betula* spp., aspen, *Populus tremula*, rowan, *Sorbus aucuparia,* and willows, *Salix* spp. Within the boreo-nemoral zone, the occurrence of hard wood trees increases, including elm *Ulmus glabra*, ash *Fraxinus excelsior*, oak *Quercus alba*, lime/linden *Tilia cordata*, maple *Acer platanoides* and beech *Fagus silvatica*. The proportion of pine generally increases towards the north, while agricultural land and deciduous species decrease. Forests are typically logged with a rotation period of 80-100 years. In all locations, the field layer is comprised of dwarf shrubs such as blueberry, *Vaccinium myrtillus* L., lingonberry, *V. vitis-idaea*., black crowberry, *Empetrum nigrum* ssp. *hermaphroditum* (Lange ex Hagerup) Böcher, sedges, *Carex* spp., grasses, *Poaceae* spp., and dwarf birch, *Betula nana* in the northern locations.

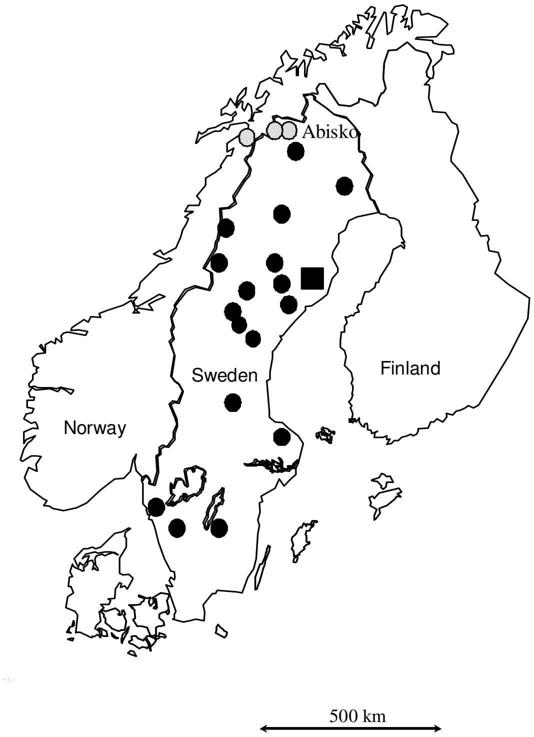


Figure 2. Study area showing the 21 locations included in the thesis. The three northernmost locations (grey) were used in Paper IV. The black square shows the Robertsfors location used in Paper I. Paper II and V were conducted only in the Abisko area. All locations except the two most northwestern areas (grey) were used in Paper III.

Methods

All studies included in the thesis were based on free-ranging moose, almost all individually marked. The moose were immobilized between 1990 and 2007, with Ethorphine and Xylazine (Sandegren *et al.*, 1987) using a dart gun (Model 1M, Daninject) from helicopters. Each animal was marked with unique ear-tags, and most moose were also equipped with a radio collar (Televilt International, Lindesberg, Sweden). The locations of radio-collared moose were determined by triangulation, and the centre of their home ranges were calculated using the adaptive kernelling (Worton, 1989) option of the program Tracker (Camptonus AB, 1994).

Distance between summer and winter ranges was defined as the straight-line distance between the centroids of the ranges. Moose were classified as migratory if the minimum convex polygons (White and Garrott, 1990) for its winter and summer areas during consecutive years did not overlap.

Table 1. Climate characteristics for study sites. The table show coordinates (lat., long.), mean monthly temperature (°C) and precipitation (mm) during the three warmest summer months (June, July, August) and the three coldest winter months (December, January, February), together with mean snow depth for the months with the deepest snow cover (January, February, March), and duration of snow cover (days with snow on the ground). In the table, study locations are sorted by descending latitude from Abisko in the north, to Mark in the south.

Study site	*Coordinates*	*Vegetation zone*	*Summer temp.*	*Winter temp.*	*Summer prec.*	*Winter prec.*	*Snow depth*	*Duration of snow*	*Seasonality*
Abisko	68°21'N, 18°49'E	Alpine	9.70	-10.60	40.33	304	47.2	225	137.92
Puoltsa	67°47'N, 19°51'E	Middle-boreal	10.23	-15.20	62.00	467	75.7	225	90.79
Överkalix	66°16'N, 22°50'E	Middle-boreal	13.60	-12.97	53.67	533	65.0	175	124.02
Arjeplog	66°15'N, 17°57'E	North-boreal	11.57	-12.83	70.67	554	66.2	200	113.15
Hemavan	65°43'N, 15°15'E	Alpine	10.33	-11.97	65.67	661	81.2	200	95.06
Malå	65°11'N, 18°45'E	Middle-boreal	12.73	-12.03	66.33	552	67.8	200	115.11
Robertsfors	64°12'N, 20°45'E	Middle-boreal	13.37	-8.97	62.33	595	40.3	150	113.39
Hällnäs	64°17'N, 19°34'E	Middle-boreal	13.17	-11.00	67.00	562	58.0	175	107.15
Bågede	64°26'N, 14°43'E	North-boreal	10.50	-9.10	77.67	664	65.7	200	107.74
Åsele	71°18'N, 15°77'E	Middle-boreal	12.47	-11.20	66.00	561	56.7	175	117.89
Junsele	63°38'N, 16°17'E	Middle-boreal	13.27	-8.80	70.67	586	51.3	150	93.80
Nordmaling	63°34'N, 19°25'E	Middle-boreal	13.80	-8.30	59.00	651	45.2	150	102.21
Ramsele	63°41'N, 16°52'E	South-boreal	13.37	-10.67	64.67	551	49.3	150	107.21
Långsele	63°10'N, 17°40'E	South-boreal	14.00	-9.27	59.67	499	33.7	150	141.10
Orsa	61°30'N, 14°51'E	Middle-boreal	13.07	-9.03	88.00	751	51.7	175	109.97
Gimo	60°85'N, 18°11'E	Boreo-nemoral	14.90	-4.27	64.33	608	22.5	100	105.51
Uddevalla	58°22'N, 11°56'E	Boreo-nemoral	15.53	-2.07	75.33	873	13.8	50	92.35
Aneby	57°53'N, 14°44'E	Boreo-nemoral	14.03	-3.43	60.33	610	76.0	100	113.31
Mark	57°32'N, 12°28'E	Middle-boreal	14.93	-2.10	80.67	917	13.5	75	113.22

To evaluate the composition of each moose's home range, systematic line-transect sampling was performed within moose ranges of 36 migrant and 30 resident moose within the Robertsfors location, and 9 migrant moose within the Abisko location. The composition of the vegetation was estimated along the transects, including tree species in both study locations, and the occurrence of clear cuts, mires, agricultural fields, and lakes within the Robertsfors location. For pine, stands between 5 and 30 years of age were included in the analyses to ensure that all important pine areas were considered, because the maximum browse production of pine is between 15-20 years (Bergström and Hjeljord, 1987). Pines were not present in more than trace amounts at the Abisko location. Snow depth was measured in year-round ranges of residents, and in winter and summer ranges of migrant moose. Both ranges of a given migrant were examined on the same day so that snow conditions in winter ranges *vs*. summer ranges were not confounded by changes in temperature or precipitation. When moose tracks were encountered along thetransects in the Robertsfors location, the depths of the tracks were measured from the top of the snow layer down to the bottom of the footprint. Sinking depths of calves and adults were separated and treated as two potential indices of snow quality ("effective snow depth"), because foot loading is much greater for adults than for calves (Kelsall and Prescott, 1967). Within the Robertsfors location, sinking depths alone were used to assess snow quality, but in the Abisko location, snow density estimates were further refined by calculating the force per unit area (kg/cm^2) needed to reach the depth equal to the moose footprint (see the section below for methods used to estimate snow quality).

Behaviour in varying snow conditions

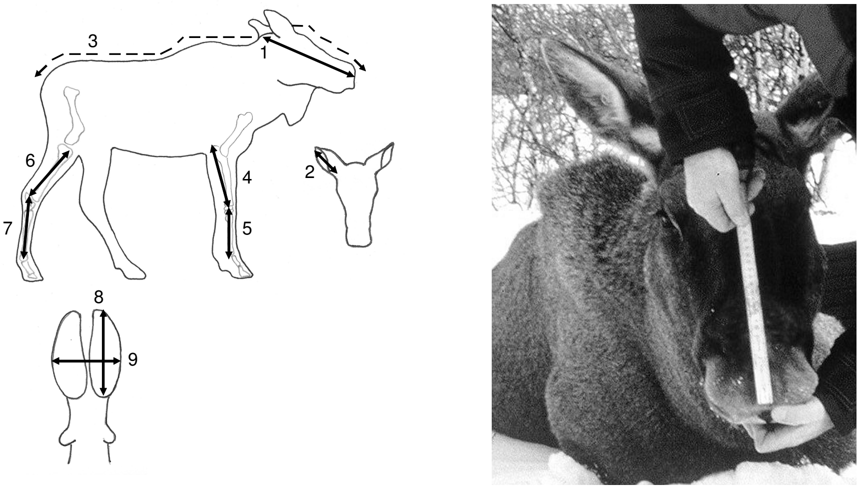
To study the behavioural response of moose to variations in snow conditions, fresh (2 – 10 min old) footprints from free-ranging moose (37 adults and 31 calves) were examined in the Abisko location. The proportion of trail-following behaviour (*i.e.* placing their feet in the footprints previously made by other moose, see Figure 3) was recorded along each trail for a total of 258 and 145 tracks of adults and calves respectively.

Figure 3. Moose following behaviour. Note that the second moose is placing its feet into the footprints of the one making the trail, thus saving valuble energy needed for winter maintenance. Photo: Eric Andersson.

The properties of the snow were measured immediately adjacent to the footprints, and the depth of the footprint was measured to the nearest cm. To assess snow quality, a mechanical dynamometer (PIAB model DT/DTN 300, CA Mätsystem AB, Täby, Sweden) attached to a steel extension rod with a replaceable circular disc on the other end of the rod was used to and measure the force required to press the disc down through the snow to the depth equal to that of the adjoining footprint. Snow quality was then indexed by calculating the force per unit area (kg/cm^2) needed to reach the depth equal to the moose footprint. The occurrence and location of any harder layers within the snow pack was also recorded, and total snow depth was measured to the nearest cm. In addition to snow properties, altitude, snow and air temperatures, and the vegetation coverage at the site of the moose trails was recorded.

Morphology in relation to climate

Moose morphology was studied on 1435 live free-ranging moose in 19 different study locations. The morphological measurements included rostrum length (*i.e.* head length), total body length, ear length, leg length, and the length and width of the hooves (Figure 4). Hoof size was calculated by using the formula for an ellipsoid, which most resembles the shape of a real moose hoof. Weight load was calculated by dividing body mass by the total area of the four hooves (Telfer and Kelsall, 1979). Leg length was measured by adding the length of the cannon bone (radius and ulna fused), to the length of the metacarpus for fore legs, and the length of the shin bone (tibia) to the length of the metatarsus for hind legs. The length of front legs and hind legs was then used as a measure of average leg length.



4a

4b

*Figure 4*a) Moose morphology measurements (cm). 1. Rostrum length, 2. Ear length, 3.Body length, 4. Cannon bone, 5. Metatcarpus, 6. Shin bone, 7. Metatarsus, 8. Hoof length. 9. Hoof width. b). Immobilized moose being measured in the field. Photo: C. Lundmark.

Age was determined by tooth wear (Skunke, 1949). Live body mass was measured by manoeuvring the moose onto a tarpaulin attached to a scale suspended from the helicopter. In addition to immobilized moose, morphological data was retrieved from moose killed by car or train collisions at the Abisko location. For moose that were later shot by hunters, or otherwise dead, the age estimate was improved by counting the number of annual cementum layers of the first molar (Bubenik, 1998). Since size varies with age (Sand *et al.*, 1995; Schwartz, 1998;), we used the Gompertz growth equation (Zullinger *et al.*, 1984; Sand *et al.*, 1995; Moscarella *et al.*, 2001) to control for differences in size with age among capture locations because age structure may vary among locations

Foraging conditions during winter

Quality and availability of forage was studied within the three northernmost study locations: Abisko, Vassijaure, and Skjomdal. The vertical distribution of quality and biomass of annual shoots were studied by cutting 24 birch and 23 willow trees at the bite diameter exhibited by moose in the area. The concentrations of secondary defence compounds (phenols and tannins) were analysed using the Folin-Ciocalteau reagent method (Waterman and Mole, 1994; Shofield *et al.*, 2001), and fibre content was analysed on a subset of the shoot samples using acid detergent fibre (ADF) extraction (Mould and Robbins, 1981) and a near infrared spectrophotometer (NIR System Process Analytics 6500) and interpolated to the total sample set (Foley *et al.*, 1998). The effect of snow accumulation on forage availability was studied in randomly-selected trees of birch and willow, after every snowfall of more than five cm during the 1997/1998 winter.

To test one of the most widely-used foraging models regarding herbivores feeding in food concentrated patches (Spalinger and Hobbs, 1992) forage intake was studied in the Abisko location between January and April 1999. The durations of 21 and 15 entire foraging bouts of free-ranging adults and young were measured. Of these, detailed studies of bites and chews were analyzed for 9 adults and 4 young, from distances of 5 to 30 m. In total, foraging bouts of adults and young comprised 843 and 386 minutes for adults and young respectively. Later, analyzing the videotapes, lengths of bite and chew sequences were carefully measured, and the number and rates of bites and chews were counted and calculated. Dry matter intake was calculated from the sizes and numbers of twigs eaten and the relationship between length and biomass of birch and willow twigs collected within the study area (n = 107 for each species). To relate the observed foraging behaviour to the Spalinger-Hobbs (1992) model, we applied the observed mean values of bite size (*S*) bite rate (*h*), and maximum chewing rate (R_{max}) to the foraging model (Eq.1), thus tentatively presuming that the underlying assumptions of the model were valid (*i.e.* that the foraging parameters do not change with time). Next, to compare the above intake with intake incorporating changes with time, we applied the linear regression equations derived from these changes to the model. Finally, intake rates were calculated using data from the first 10 minutes of the foraging bouts, as a way to compare the intake estimates given by using data obtained from entire foraging bouts with the results given by using only data from short-term trials (*e.g.* 10 min.).

Results

Migration and habitat selection (Paper I, II)

Vegetation composition

The results of the study of seasonal ranges in the Robertsfors location showed that home ranges were not much different in the composition of the vegetation, regardless if moose were migrant and moved between summer and winter ranges, or if they were resident and stayed within the same area. Comparing between ranges of migrant and resident moose, the only difference found was that winter ranges of migrants had less agricultural fields than did residents' ranges.

For migrants, winter ranges were not different in terms of vegetation from the summer ranges they left. This pattern was also noted within the northernmost study location (Abisko), where the results showed no difference between seasonal ranges at tree-stand level (here, birch and willow, $p > 0.13$, unpublished data).

Concerning habitat selection at lower levels (*i.e.* within the home ranges), moose preferred ranges with a lower proportion of open habitats (mires, clear cuts, and fields), while ranges with deciduous trees were neither preferred nor avoided (Table 2). There was also a tendency for moose to choose ranges with more pine and spruce.

Snow conditions

Comparing winter ranges of migrants to the year-round ranges of residents in Robertsfors, there was no significant difference in snow depth *per se*. In fact, there was even a tendency for deeper snow in winter ranges of migrants than in ranges of residents (p=0.08). Within home ranges, moose preferentially used ranges with less snow (p=0.04, Table 2).

In the northernmost study location (Abisko) however, the results differed from those in Robertsfors. In this mountainous region, snow depth was important, as winter ranges of migrant moose had significantly less snow than summer ranges (80.0 *vs*. 56.2 cm, p > 0.01).

Snow quality (as indexed by sinking depths of moose) differed between ranges of migrants and residents in the Robertsfors location, as migrant calves sank significantly less deep into the snow at their winter ranges than what resident calves did (p=0.007). For adults, sinking depths did not differ between ranges. In the Abisko location, snow quality did not vary between seasonal ranges (p>0.09).

Table 2. Comparison of snow depth (cm) and habitat characteristics (%) at used vs. available areas within home ranges of individual moose in Robertsfors (n=66 moose: 36 migrants and 30 residents).

	Used areas		*Available areas*	
	Mean	*SE*	*Mean*	*SE*
Snowdepth	51.5	3.07	59.2	1.79
Mire	0.12	0.38	0.18	0.02
Pine	6.84	0.24	6.69	0.11
Spruce	5.13	0.01	4.14	0.01
Deciduous	1.89	0.01	1.70	0.01
Clear cut	0.01	0.41	0.04	0.19
Field	0.14	0.54	0.04	0.24

Sinking depths of moose were to a large extent be explained by snow quality, which emerged as the most important factor when selecting among multiple competing models (Table 3a) Snow quality was also involved in the best model when combining several environmental variables (*i.e.* snow depth, altitude, and air temperature) to explain sinking depth (by using AIC-analyses). The effects of air and snow temperature may be explained by their indirect influences on snow metamorphosis, and that ranges situated at higher elevations had deeper snow (which was more supportive, $p < 0.01$ in bivariate correlations). Snow depth *per se* was only the third important single variable in affecting sinking depth, and it did not emerge at all in the best model when combining several variables.

The study of following behaviour showed no strong effect of either snow depth, snow quality, nor sinking depth on the extent to which moose followed in the tracks of other moose (Table 3b). Instead, following behaviour seemingly responded to the temperature of the air, possibly due to the effects of temperature on snow quality (snow density increased significantly with increasing temperatures).

a)

AIC	*Δ*	*R*	*W*	*Variables in Model*
298.75	0.00	0.16	0.37	snow quality
298.85	0.10	0.16	0.35	altitude
299.40	0.66	0.16	0.26	snow depth
305.23	6.48	0.08	0.01	snowtemp
307.70	8.95	0.04	0.00	air temperature
309.27	10.52	0.02	0.00	coverage

b)

AIC	*Δ*	*R*	*W*	*Variables in Model*
397.27	0.00	0.05	0.33	airtemp
398.84	1.57	0.02	0.15	altitude
399.17	1.91	0.02	0.13	snow depth
399.20	1.93	0.02	0.13	snowtemp
397.27	0.00	0.05	0.33	airtemp
398.84	1.57	0.02	0.15	altitude

Table 3. AIC-table for a) sinking depths (the depth of the footprints), and b) following behavior (the proportion of a 200m moose trail when moose put their feet exactly in the footprints of other moose). Models are sorted by Akaike weights (*W*), and also show the difference in AIC values between the models (Δ), as well as the r-square (r) for the variables used in the model: snow depth, snow quality (as indexed by the force needed to press a simulated moose foot down to the depth of a moose footprint), snow temperature, sinking depth, air temperature, vegetation coverage, and altitude.

Morphology in relation to snow

Moose morphology was more closely linked to snow conditions than to environmental temperature or latitude. In locations with more severe snow conditions, moose had significantly larger hooves and longer legs than that expected by their size.

Weighing the relative importance of the duration of snow cover *vs.* snow depth, the results indicated that the most important variable to hoof area was the duration of snow cover. Weight load did not follow the snow-coping hypothesis.

Heat conservation and heat stress

Moose body mass supported the original proposal of Bergmann, thus describing a relationship of climate to body mass alone, not surface area in relation to body mass (Bergmann, 1847 in Mayr, 1963). Body mass of moose was also related to seasonality, but the test of the competing hypotheses (Bergmann's rule *vs.* the seasonality hypothesis, Table 4) revealed that the evidence for the seasonality hypothesis was weaker than for Bergmann's rule (both mass and body length were more related to annual temperature and latitude).

Table 4. Testing between the competing hypotheses of heat conservation (Bergmann's rule), and the seasonality hypothesis. The magnitude of the F-values (bold face) indicate that annual temperature is the stronger predictor of both body mass and body length after controlling for inter-correlations among the three predictor variables. A "yes" in the columns indicates that the sign of the correlation was as predicted by the hypothesis; a "no" would mean that the correlation was in the opposite direction, thus not supporting the hypothesis at all). Bergmann's hypothesis is supported over the seasonality hypotheses.

Heat conservation vs. Seasonality hypotheses

		Seasonality		*Heat conservation (Bergmann's rule)*			
				Latitude		*Annual temp*	
Females	Body mass	0.07 (0.80)	yes	0.46 (0.52)	yes	**3.35** (0.11)	yes
	Body length	0.01 (0.92)	yes	0.11 (0.75)	yes	**0.37** (0.55)	yes
Males	Body mass	0.04 (0.84)	yes	0.00 (0.96)	yes	**1.38** (0.29)	yes
	Body length	0.05 (0.83)	yes	0.12 (0.74)	yes	**0.82** (0.38)	yes

Although lengths of both rostra and legs were related to heat stress, the direction of this relationship was not in line with the heat stress hypothesis since they were in fact shorter in warm summers. The observed pattern in rostrum lengths and leg lengths also strongly falsifies the heat-conservation hypothesis (and thus also Allen's rule), as both legs and rostra were longer in areas with cool winters (Table 5).

Table 5. Testing between the competing hypotheses of heat conservation (Allen's rule) and the heat stress hypothesis. F- and p-values (within brackets) are the effects of the individual climate variables in the general linear model (thus controlling for the correlation between summer and winter temperature). Values in bold indicate the larger F-values if in the direction predicted by the hypothesis. A "yes" below indicates that the sign of the correlation was as predicted by the hypothesis; a "no" means that correlation was in the opposite direction, thus not supporting the hypothesis at all. Weighing the relative support for the competing models by comparing the F-values, the heat stress model is favoured over the heat conservation model because ear lengths exhibited the pattern expected for the former (however, ears were also shorter in areas with cold winters).

Heat conservation vs. Heat stress hypotheses

		Heat stress (summer temp)		*Heat conservation(winter temp)*	
Females	Ear length	**0.51** (0.49)	yes	0 15 (0.71)	yes
	Rostrum length	0.16 (0.70)	no	0.09 (0.77)	no
	Leg length	0.01 (0.91)	no	1.08 (0.31)	no
Males	Ear length	**0.07** (0.80)	yes	0.00 (0.97)	yes
	Rostrum length	3.94 (0.07)	no	0.09 (0.77)	no
	Leg length	1.09 (0.77)	no	1.38 (0.26)	no

Quality and availability of winter forage (Paper IV)

Accumulating snow had little effect on forage availability, at least for the larger herbivores such as the moose. Although snow had significant effects at the lower parts of the trees, most of the forage was found above the mean snow depths, and still within the reach of herbivores.

Analysis of the vertical distribution of biomass of birch and willow revealed that most of the willow biomass (87%) was found within the browse height of moose. Willows was thus of greater accessibility to moose than birch, even though the total biomass of birch browse within trees was greater. Considering now overall forage quality between birch and willow, birch had higher concentrations of nitrogen and secondary defence compounds than willow, but less fibre. The vertical distribution showed the same pattern for both forage species: concentrations of nitrogen increased with height, and fibre decreased. The concentration of non-tannin phenols increased with height of willow, while tannins decreased with height of birch. Our results thus indicate that the best forage is found at the top of birch trees, and at the middle to top levels of willow, which also has more available food in the middle heights, which is easily accessible to herbivores.

Foraging in winter (Paper V)

The average moose in the Abisko location spent more time in resting and bedding activities (86 and 98 min for adults and young respectively) than in moving and/or feeding activities (72 and 80 min). Although adult moose spent a smaller proportion of their active time in feeding than young moose (48 % *vs.* 63 %), they fed more intensively than young moose by using more time per bite and chew. Adults also took almost twice as many bites of willow compared to birch (1091 *vs.* 576), even though feeding on birch appeared more time consuming than feeding on willow, as birch needed longer chewing time. In this study, young moose were not studied when feeding on birch.

The feeding behaviour of moose changed over the duration of a foraging bout, as moose bit and chewed more slowly with increasing sequence length, and young moose also took smaller bites the longer a sequence lasted, thus leading to reduced intake rates (Figure 5).

The underlying assumptions of foraging model (regarding invariance of bites and chews with time) did therefore not hold when being tested on free-ranging moose feeding at their own choice during winter. As a consequence, the Spalinger-Hobbs (1992) foraging model underestimated intake of willow by 17% for adults and 23% for young moose, while intake of birch was overestimated by more than double (107%). The higher quality willow had more available forage within the browse height of moose, compared with birch (as shown in Paper IV), which also may add to making willow the “faster food”, since more food is easily available compared to birch.

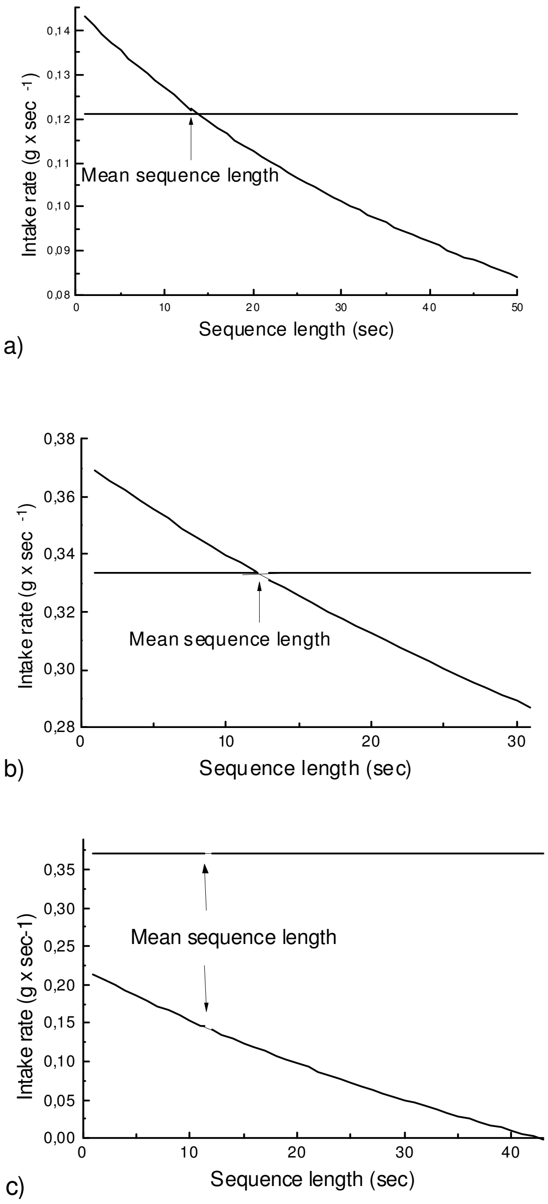


Figure 5. Intake rate vs. bite and hew sequence lengths for a) adult moose feeding mountain birch, b) adults feeding on willow, and c) young moose feeding on willow. The curves show the intake rates calculated by the Spalinger-Hobbs (1992) model incorporating the observed changes with time in bite size an rates of bites and chews. The horizontal line shows the intake rates calculated by the model assuming that the assumptions of the model are valid (i.e. that no variables change with time. Mean sequence lengths are indicated by an arrow.

Intake rates calculated by using data from only the first 10 min of the foraging bouts overestimated intake of birch by adults 31%, and underestimated intake of willow for both adults (24%) and young (15%), compared with intake calculated using data from entire bouts (Figure 6).

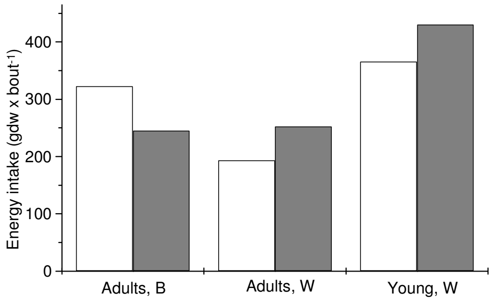


Figure 6. Forage intake (gdm, grams dry mass) calculated for foraging bouts of moose feeding on birch (B) and willow (W). The figure shows intake calculated by applying data obtained from the first 10 min of a foraging bout (white) and intake calculated from data obtained from an entire bout (grey

General discussion

Effects of snow on behaviour and morphology

Seasonal migration and habitat choice

The behaviour of free-ranging ungulates reflects trade-offs among a wide range of factors, such as foraging and digestive efficiencies, food availability and quantity, changes in body mass and condition, and environmental variations in climate and snow conditions. The effects of snow on moose migration differed between the Robertsfors and Abisko locations. In the northernmost study location (Abisko), the results showed that snow depth was important, as winter ranges of migrant moose had significantly less snow than summer ranges (Paper II). Here, the topography is highly variable, and snow depth varies dramatically in short distances because of the mountains causing a "precipitation shadow" (mean snow depth 55.7 cm, range 2 – 245 cm), and moose may therefore greatly benefit by migrating even short distances. Heavy snowfall events have been documented as being associated with moose leaving their summer ranges to migrate towards winter ranges in ranges with less deep snow (Ball *et al.*, 1999), and moose in the Abisko location have frequently been observed to behave similarly. In the Robertsfors location however (Paper I), snow depth was not important in selection of winter ranges. This trend is in the opposite direction of what might be expected if a benefit of migration is a winter range with less snow than that experienced by a non-migrating animal, and migrant moose in this location does thus not appear to benefit by having winter ranges with less snow than their summer ranges, nor with less snow than resident moose. In this coastal region, differences in snow depth and precipitation within the location are smaller compared to Abisko (mean snow depth 59.2 cm, range 35 – 100 cm), but snow depths should still be enough to allow a rather powerful test, especially since depths of 40 to 50 cm are generally associated with moose leaving their summer range (Coady, 1974; Sandegren *et al.*, 1985). Although snow depth was not important in selection of seasonal ranges in the Robertsfors location, it affected habitat selection at a smaller scale (*i.e.* within seasonal ranges), as moose preferentially used sites with less snow. These results show that snow conditions may be important for habitat selection, but that it may vary between different ranges both at large (*i.e.* geographically separated locations such as Abisko and Robertsfors) and smaller scales (*i.e.* when selecting sites within home ranges).

The variability in results regarding snow depths *per se* indicated that other aspects of snow may be involved in behaviour of moose, and Paper I shows that snow quality may influence the selection of winter ranges in the Robertsfors location. Here, calves of migrant moose calves sank significantly less deep into the snow at their winter ranges than what resident calves did, thus indicating that snow was of higher quality at ranges of migrants. Compared to residents, migrants may thus benefit by migrating to ranges with less snow, as sinking depth is important by directly determining how much energy an animal has to spend when moving. For adults, sinking depths did not differ between ranges, which might be because foot loading increases greatly with age (Kelsall and Prescott, 1967). It may thus be that it was only the sinking depths of calves that was a sensitive enough measure to reveal small differences in snow quality between ranges. Adults, with their heavier foot loading, may thus have been too crude a measure for this initial study on snow quality. In the Abisko location, snow quality did not differ between seasonal ranges (perhaps because of generally colder and drier climate in the north), so at this location it seems that it may be the large differences in snow depths that drive the seasonal migration of moose. In summary, areas with less variable snow depths, snow quality emerges as one of the possible snow variables involved in seasonal migration, while in areas with more variable snow depths, migration may be driven by snow depths alone (or in association with snow quality).

Sinking depths and following behaviour

To further study the importance of snow conditions, sinking depths of a simulated moose hoof was used to more precisely index snow quality (Paper II). Here, snow quality emerged as the most important variable in affecting sinking depths, and snow quality was also involved in the best model when combining several environmental variables. The importance of snow quality most likely relates to its effect on the energetic effects of sinking depths on energy costs while walking in snow. The results strongly suggest that the traditional view of snow conditions by measuring snow depth *per se* may thus not be enough. In fact, snow depth was only the third important single variable in affecting sinking depth, and it did not emerge at all in the best model when combining several variables. When examining the other variables included in the best combined model regarding sinking depths (air temperature and altitude), the effects of air and snow temperature may be explained by their indirect influences on snow metamorphosis (snow quality increased significantly with air temperature, and that ranges situated at higher elevations had deeper snow which was more supportive (snow quality increased significantly with snow depth).

The study of following behaviour showed no strong effect of snow depth, snow quality, nor sinking depth on the extent to which moose followed in the tracks of other moose. Instead, following behaviour seemingly responded to the temperature of the air, possibly due to the effects of temperature on snow quality (snow density increased significantly with increasing temperatures). Behavioural decisions such as choosing if and when to walk in the footsteps of another animal thus are more difficult to explain than the direct measurements of sinking depths *per se*, and it may be necessary to combine several variables in addition to snow. The paradoxical importance of snow quality (reducing the energy cost in some cases by decreasing sinking depths, but in others increasing it by forcing the animal to work harder when moving through crusted snow) may partly explain why we did not detect stronger evidence for the importance of snow quality for following behaviour. As also noted in previous studies (Johnson and Marks, 2004), snow quality is notoriously difficult to quantify, especially in late winter when snow approaches the melting temperature.

Morphology in relation to snow

In paper III, the analysis revealed evidence of variation in moose morphology among locations, and that moose morphology was more closely linked to snow conditions than to environmental temperature and latitude. Moose had significantly larger hooves and longer legs in locations with more severe snow conditions. Since moose were not significantly larger in more snowy areas, the larger hooves could not simply be explained by correlations between hoof size and body size. Hoof size may thus be the most direct response to snow-induced morphological selection.

The longer legs of moose in locations with deeper snow corresponds to the general pattern that animals living in snow often possess disproportionately long limbs in comparison to those in less snowy areas (*e.g.* Coady, 1974; Telfer and Kelsall 1984; Fancy and White, 1987; Klein et al., 1987; Marchand, 1991; Murray and Boutin, 1991). The results regarding leg lengths thus show stronger support for the snow-coping hypothesis than hypotheses relating morphology to temperature or seasonality, and suggest that snow is more important than temperature in shaping the morphology of northern ungulates (Garroway and Broders, 2005).

Weight load did not follow the snow-coping hypothesis (*e.g.* that moose are morphologically adapted to snow, by for example having less foot load in snowy areas). The relationships between weight load and snow conditions was perhaps the most difficult factor to assess in this study, since many factors such as weight, speed, type of location, and behaviour are involved in determining the actual weight an animal places on each hoof (Kelsall and Prescott, 1967). Perhaps most importantly, moose can voluntarily increase hoof area by spreading the digits of the hooves, and thereby decrease weight load when walking on soft surfaces (Coady, 1974). As indicated in previous studies (Van Voorhies, 1997), snow-induced selection is far from consistent among northern populations, but may vary due to differences in the ability to cope with snow by other means of adaptation (such as migration, habitat choice, or following behaviour), or by differences allocating energy during the snowy season (*i.e.* by forage intake, heat conservation, and behaviour). In addition, differences in snow conditions may have several causes, and moose may in fact be responding to one of these other factors, such as the density and composition of the vegetation, and exposure to wind and sunlight.

Morphology in relation to temperature, latitude, and seasonality

Heat conservation and heat stress

If moose conform to the rules of Bergmann and Allen, an “optimally designed” animal in a cold snow-free location should be large and have short thick legs in order to conserve heat, while in a warmer location with deep snow, body size should be small and legs longer. However, animals are generally shaped by a variety of demands acting on energetics and survival (sometimes even contradicting demands), so a simple universal explanation for the relationships between temperature and body size should not always be expected. The results shown in Paper III supported Bergmann’s rule (with respect to body mass), and are thus in accordance with the original proposal of Bergman, describing a relationship of climate to body mass alone, not surface area in relation to body mass. This pattern regarding the relationships between body mass of moose and environmental conditions has also previously been reported for moose in Scandinavia (Solberg *et al.*, 1999; Herfindal *et al.*, 2006a,b). In addition to temperature, body mass of moose was also related to seasonality, but the test of the two competing hypotheses (Bergmann’s rule and the seasonality hypothesis) revealed that the evidence for the seasonality hypothesis was weaker than for Bergmann’s rule.

The only extremities that followed Allen’s rule were the ears. For Allen’s rule to be important, the extremities have to be sites of substantial heat loss or we would expect little natural selection to have occurred. Northern mammals such as the moose often show strong physiological adaptations to low temperatures (such as heat exchange between veins and arteries in the legs and a very isolative winter hair coat, Geist, 1987; Marchand, 1991). For cold-adapted animals like the moose, legs may thus not be as great a source of heat loss during winter as one might expect given their length. Although lengths of both rostra and legs were related to heat stress, the direction of this relationship was not in line with the heat stress hypothesis since they were shorter in warm summers. The observed pattern in rostrum lengths and leg lengths strongly falsifies the heat-stress hypothesis (and also Allen’s rule as they were longer in areas with cool winters). The unexpected pattern in our results regarding temperature/latitudinal adaptations may thus be a result of the multiple environmental demands on moose living at high latitude locations and may be driven by selection for long legs in deep snow, regardless of thermal costs.

Migration and vegetation composition

If migration is adaptive, it must involve some positive change in the moose's environment to compensate for the cost of travelling between the seasonal ranges. In partially migratory populations (such as moose populations north of 60°N), one possibility is that both migrants and residents use similar ranges during a given season, but then migrants move to areas which are better in some way during the other season. The results of the study of seasonal ranges in the Robertsfors location (Paper I) showed that home ranges were not much different in the composition of the vegetation, regardless if moose were migrant and moved between summer and winter ranges, or if they were resident and stayed within the same area. This pattern was also noted within the northernmost study location (Abisko), where the results showed no difference between seasonal ranges at tree-stand level (here, birch and willow, $p > 0.13$, unpublished results). Overall, there was thus little evidence that seasonal migration served to move moose between ranges which differ in the composition of their vegetation per se. Concerning habitat selection at lower levels (*i.e.* within the home ranges), the results showed that moose did select certain habitat types (thus suggesting that our sample sizes were adequate). Moose preferred ranges with a lower proportion of open habitats (mires, clear cuts, and fields), while ranges with deciduous trees were neither preferred nor avoided. There was, however, a tendency for moose to choose ranges with more pine and spruce.

Foraging behaviour and the quality and quantity of winter forage

The quantity and quality of twigs of annual growth differed between birch and willows (Paper IV). Willows were of greater accessibility to moose than birch, even though the total biomass of birch browse within trees was greater. Willows also had lower concentrations of secondary defence compounds and nitrogen, than birch, but more fibre. The inter-specific differences appeared to affect intake of winter browse - in Paper V, moose were observed to take almost twice as many bites of willow compared to birch, even though birch needed longer chewing times, and thus were more “time consuming” to ingest than willow. The results in Paper IV thus support the results of previous studies that herbivores prefer the species with lower concentrations of secondary defence compounds (Rousi et al., 1991; Stolter *et al.* 2005), and that nitrogen may be of lesser importance in the choice of browse species during winter (Palo et al., 1997; Shipley *et* *al.*, 1998, Stolter *et al.* 2005). The vertical distribution of nitrogen and fibre showed the same pattern for both forage species: concentrations of nitrogen increased with height, and fibre decreased. The concentration of non-tannin phenols increased with height of willow, while tannins decreased with height of birch. Our results thus indicate that the best forage is found at the top of birch trees, and at the middle to top levels of willow. Consistent with this, the analysis of the video-tapes of foraging moose (Paper V), revealed that moose most commonly fed at height between 1.5 and 3.5 m (unpublished data), and were rarely observed to feed at lower levels of the trees where the lesser quality food is found. Moose also frequently feed on the top of felled trees when available (Danell *et al.*, 1990), thus gaining the benefits of the availability of high quality food that is normally out of reach.

The differences in quality and availability of forage between forage species were also evident when testing the Spalinger-Hobbs (1992) foraging model (Paper V). Under the assumptions that model parameters were invariant during the course of a foraging bout, the model underestimated intake of willow and overestimated intake of birch. As shown in Paper IV, the higher quality willow (lower levels of secondary defence compounds) also had more available forage within the browse height of moose, compared with birch, which also may add to making willow the "faster food", since more food is easily available compared to birch. The results of Paper V regarding intake rates coupled with the results of Paper IV regarding forage quality thus show that intake rate declines with decreasing forage quality, and the results thus agrees with previous findings that less digestible forage needs to be chewed longer and takes longer to digest (Shipley and Spalinger 1992; Bergman *et al.*, 2001). The differences in forage quality play a central role in foraging theory (Searle *et al.*, 2005), and is caused by multiple factors, including reductions in bite mass and prolonged bite rates of the lower quality forage, rather than in time allocated to actually cropping (biting) the food.

The results regarding the vertical distribution of quantity and quality of forage (Paper IV) and foraging rates (Paper V) thus agree with the qualitative predictions of optimal foraging theory: that herbivores in general prefer to feed on forage with higher quantity and quality of food. Here, moose feed predominantly on the higher quality and more abundant willow, but also to a great extent on birch which had more nitrogen, but also more secondary defence compounds. In nature, where there commonly is a great diversity of plants, animals can cope with secondary defence compounds and variations in nutrient concentrations by eating a variety of forage species (Stolter *et al.*, 2005; Provenza *et al.*, 2007), and by choosing between different parts of the plants. The complex distribution of forage in the wild may thus make it beneficial for large herbivores to show intermediate selectivity, rather than foraging on only the highest quality food possible (Alm *et al.*, 2002; Simpson *et al.*, 2004). Moose at high latitudes (where there are few forage species to choose among during winter), should thus make the best use of the available forage: birch for its high nitrogen content, and willow for its generally low concentrations of secondary defence compounds. Selecting the most favourable forage will ultimately allow moose to deposit more fat and protein, which may be of substantial importance in terms of winter survival (Moen *et al.*, 1997).

The test of the Spalinger-Hobbs (1992) foraging model (Paper V) revealed that forage intake changed with time, and also that intake rates calculated by using data from only the first 10 min of the foraging bouts greatly mis-estimated forage intake. The intake of birch was overestimated, and willow intake was underestimated. This study thus suggests that, unless the model is parameterized by observing complete foraging bouts, intake rates may be mis-estimated by enough to be important to ecologists employing the Spalinger-Hobbs (1992) model to understand the ecology of free-ranging ungulates with long foraging bouts like the moose.

Conclusions

In this thesis, I combined variables relating to climate and foraging conditions and studied behaviour and morphology of moose. The thesis highlights the importance of considering the relationship between the above variables, as they are all more or less inter-correlated.

The study of seasonal migration and habitat choice showed that the effect of snow depth per se differs between locations depending on variations in snow severity: in locations that show large differences in snow depths within rather short distance, snow depth is important, but in locations where snow depth is less variable snow quality emerges as the more important factor. So far, the importance of snow quality for seasonal migration, habitat choice, and behaviour is far less studied than the importance of snow depth, perhaps due to the difficulties in quantifying snow quality. Overall, the results suggest that snow quality is involved in the habitat selection and behavioural decisions made by moose, and that snow conditions are much more important for moose migration and habitat choice than vegetation composition.

The importance of snow conditions was further highlighted in the study of moose morphology. At high latitudes with cool temperatures and severe snow conditions, moose were heavier, had larger hooves and longer legs. These morphological attributes can be seen as adaptations to deep snow (hooves and legs) and cold weather (body mass), but one must also bear in mind that moose must survive the entire year, not just the winter period so their morphology may be a compromise among several selective forces. In this study, moose both conformed to, and were in opposition to some of the most well known ecogeograhical rules (Bergmann's and Allen's). The results of this thesis regarding body mass are thus in agreement with previous studies showing that a combination of several explanatory environmental variables may be needed to understand morphological patterns, and that latitude or temperature alone is not enough. I further suggest that the approach of testing among competing hypotheses simultaneously (regarding climate variables and morphology) is the best way to the evidence among these competing hypotheses, rather than testing only one in a given study. This is because testing each hypothesis one at a time might erroneously support all hypotheses because of intercorrelations among variables (*e.g.* latitude, temperature and seasonality).

When feeding during winter, moose showed strong preference for willow over birch, but still did consume considerable birch, which is in accordance with previous studies that moose is well adapted to browsing on forage of mixed quality, and that they may balance the gains and "losses" of intake by feeding on different forage types: willow for less defence compounds, and birch for higher nitrogen levels and less fibre. Moose also have the choice to crop twigs at different parts of the trees, and can easily reach the higher quality foods at higher levels of the trees. Since calves in our study were not recorded while feeding on birch, I suggest that further foraging studies test if young moose eat lower proportions of birch than do adult moose. Furthermore, since the quality of willow browse may vary between willow species (Stolter *et al.*, 2005), future studies should ideally consider willows separately to relate the preferences of moose to the characteristics of these different willow species.

The detailed studies of foraging behaviour of free-ranging moose reported here are among the first large-scale studies of wild moose feeding at their own choice in their natural environment. The results from the test of the Spalinger-Hobbs (1992) foraging model were important, and showed that intake changed with time, and can not be assumed to be equal through the course of a foraging bout (or during a bite or chew sequence). Consequently, the assumption of parameter invariance in one of the most widely used foraging models for wild herbivores led to miss-estimations of intake that were large enough to be biologically important. In addition, the duration of the previous short term tests of the assumptions of the model are probably too short for large herbivores with long foraging bouts, compared to small herbivores for which short term trials may be reasonable. The study also show that may be important to separate between age classes of the studied herbivore, and between forage species when developing or using optimal foraging models. Based on the he results from the test of the Spalinger-Hobbs (1992) foraging model, I strongly suggest that future studies should try to obtain foraging parameters from entire foraging bouts when parameterizing the model, rather than using data from only a few minutes at the beginning of a bout (particularly if captive, food-deprived ungulates are used). Additionally, there is a need to conduct tests of animals feeding in more realistic environments, rather than on a single species of uniform density and distribution in a man-made test arena. Ideally, optimal foraging of a particular herbivore should also be studied in more than one season, as intake rate may be influenced by seasonal differences in appetite or other factors (Parker and Robbins, 1984; Parker *et al.* 1984).

Future perspectives

To understand the underlying causes of behaviour and morphology of ungulates such as the moose, both environmental conditions (snow depth, snow quality, and temperature) and forage conditions (quantity and quality) needs to be investigated further. Lately, there has been an increased interest in how animals are adapted to their environment, especially given the current rapid rates of climatic change (Post and Stenseth 1999; Post *et al.*, 2008). Global climate change has already influenced the body size and distribution of several animal species, and will likely have an even greater impact in the future (Hofgaard *et al.*, 1999; Simberloff *et al.*, 2000; Barnosky *et al.*, 2003; Parmesan and Yohe, 2003; Thomas *et al.*, 2004; Millien *et al.*, 2006; IPCC, 2008). Most models of climate change predict that northern Scandinavia will experience increased precipitation and temperature during both summer (2-4°C) and winter (3-7°C) (Kjellström *et al.*, 2005; Persson *et al.*, 2007). In the winter season snowfall may decrease due to the higher temperatures, except from high latitude areas where the increased precipitation will lead to increased snowfall (Kjellström *et al.*, 2005; Persson *et al.*, 2007). It is therefore important to further investigate how changes in snow conditions may affect northern ungulates such as the moose (Ball *et al.* 1999). The effects of snow may to a large extent depend on its quality, and thus differ largely between wet, heavy snow (that may be more supportive), and dry snow (in which animals may sink all the way through). I therefore suggest that future studies continue to evaluate the effects of varying snow quality, and further develop methods to assess snow quality directly in the field. The new method (combining several snow quality aspects into one single variable) presented in the thesis shows promise, and may be a step forward in understanding how snow is experienced by the animal.

During summer, there will not only be an increase in mean summer temperatures, but also in the number of warm days (Kjellström *et al.*, 2005; Persson *et al.*, 2007). For the heat-sensitive moose, increased temperatures will be detrimental, and moose may already show signs of being negatively affected by climate change (Van Ballenberghe and Ballard, 1998; Murray *et al.*, 2006). As changes in the environment are likely to be more important towards the edges of a species range (Davis and Shaw, 2001; Weladji and Holand, 2003), the distribution of moose may thus change, with southern populations declining, or their range withdrawing to the north (Karns, 1998; Van Ballenberghe and Ballard, 1998; Dussault, 2005; Murray *et al.*, 2006). Considering morphology, there is historical evidence that animals became smaller during warmer periods and larger during colder time periods (Smith and Betancourt 1998, 2003). Theoretically, moose could thus get smaller in a warming future, at least at their southernmost ranges. However, if the rules of Bergmann and Allen are true, they should also develop longer legs and ears to radiate heat. The results regarding the morphological patterns of moose in relation to climate are still however, somewhat unclear, and I recommend that future research investigate it further.

If we are to keep the moose population large enough for sustainable harvest in a climate changed future, we must understand how they are affected by, and adapted to, their environment. Changes in climate will most likely make some areas unsuitable as moose habitats, and render moose of lower condition and fecundity, which will reduce moose numbers, probably mostly so in the southern range of the population. In addition, moose may be shift between habitats as a response to changing climate, although when considering migration, the philopatric moose may not respond immediately by changing migration behaviour in order to find new, more suitable home ranges (Sweanor and Sandegren, 1989; Andersen, 1991a, b). Migration may thus sometimes become even mal-adaptive due to (unexpected) changes in snow conditions or food availability, since migration behaviour is maintained through several generations and appears to lag behind changes in the environment (Andersen, 1991b). To increase the accuracy of future management plans (and to minimise increased risks of browsing damage caused by moose) I therefore strongly suggest that the effects of climate (snow conditions and temperature) and forage (quantity and quality) be studied further.

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Sammanfattning

Avhandlingen fokuserar på älgens beteendemässiga och morfologiska (utseendemässiga) anpassningar till varierande snö- och klimatförhållanden. Mer specifikt behandlas säsongsbundna vandringar mellan sommar- och vinterområden, habitatval, och beteenden som leder till att minska energiåtgången då älgarna förflyttar sig inom snötäckta områden. Avhandlingen tar också upp sambanden mellan älgens morfologi, klimat, snö, och säsongsbundna klimatvariationer, samt intag, kvalitet, och tillgång på föda under vintern. Genom att videofilma frilevande älgar genomfördes ett av de mer omfattande testerna av en av de mest använda modellerna för optimal furagering,.

Resultaten belyser vikten av flera aspekter av snö, klimat och vinterföda, och visar att beteende och morfologi kan vara en kompromiss mellan flera, ibland motsägelsefulla faktorer. Studien av säsongsbundna vandringar och habitatval visade att betydelsen av snö varierar mellan olika områden beroende på variationer i snödjup. I områden där snödjupet varierar stort är det den faktor som mest påverkar vandringar och habitatval. I områden där snödjupet är mindre varierande (men fortfarande tillräckligt djup för att utlösa vandringar) är snöns kvalitet av större betydelse. Avhandlingen är därigenom en av de första att belysa betydelsen av snöns kvalitet, och gör också ett första test av en ny metod att direkt mäta snökvalitet i fält, genom att kombinera flera aspekter av snö till en enda variabel.

De jämförande studierna av olika hypoteser som används för att förklara morfologin hos däggdjur i relation till klimat och geografisk utbredning, visade att snö var av större betydelse än temperatur, latitud, och säsongsmässiga klimatvariationer. I områden med djupare och mer varaktigt snötäcke hade älgarna större klövar och längre ben än vad som kan förväntas av deras kroppsstorlek. Älgarnas morfologi överensstämde med, men stod också i motsats till de mest använda hypoteserna gällande olika djurarters storlek i förhållande till klimat och geografisk utbredning: områden med kalla vintrar var älgarna tyngre (Bergmann's regel) och hade kortare öron (Allen's regel). Detta stämde med hypoteserna att älgarnas morfologi reducerar värmeförluster i kallt vinterklimat. Resultaten visade också på visst stöd för hypotesen att älgarna är känsliga för varma temperaturer.

Kvaliten hos de två viktigaste födoslagen tillgängliga under vintern (björk och viden) varierade både inom träden och mellan trädarterna.

Viden hade mer tillgänglig föda inom beteshöjd, och lägre halter av försvarssubstanser (fenoler och tanniner) än björk, men också lägre halter av kväve, och högre fiber-innehåll. Födans kvalitet ökade med trädens höjd för både björk och viden. Skillnaderna mellan de två arterna visade sig också vid testen av Spalinger-Hobbs (1992) modell för optimal furagering. Älgarna föredrog att äta viden, som också gick snabbare att inta än björk. Resultatet av testet visade på viktiga skillnader mellan den ursprungliga modellen och det födointag som uppvisades av älgarna i studien. Modellen underskattade intaget av vide, och överskattade intaget av björk jämfört med de resultat som visades i studien. De stora skillnaderna i intag av björk jämfört med viden visade också att det är viktigt att skilja mellan födoarterna, samt mellan olika åldersklasser av djur då man ska vidareutveckla eller använda modeller för optimal furagering.

Resultaten i avhandlingen visar på behovet av fortsatta studier gällande sambandet mellan beteende, morfologi, snö och övriga klimatfaktorer, speciellt med tanke på framtida klimatförändringar. Då älgar är väl anpassade till snö- och vinterförhållanden kan både de direkta effekterna av stigande temperatur och nederbörd och de indirekta effekterna (genom påverkan på tillgång och kvalitet av föda) av klimatförändringar få negativa konsekvenser för älgstammen, speciellt i deras södra utbredningsområde.

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