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**Life history consequences  
of environmental variation  
along ecological gradients  
in northern ungulates**

Doctoral thesis  
for the degree of doctor scientiarum

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Norwegian University of Science and Technology  
Faculty of Science and Technology  
Department of Biology



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## **This thesis is based on the following papers:**

- I** Henriksen, S., **Herfindal, I.**, Aanes, R., Høgda, K.-A., Sæther, B.-E., Tveraa, T., Bråthen, K. A. & Ims, R. A. (manuscript) The relationship between satellite based vegetation indices, climate and growth of juniper in a northern ecosystem.
- II** **Herfindal, I.**, Solberg, E.J., Sæther, B.-E., Høgda, K.-A. & Andersen, R. (submitted manuscript) Environmental phenology and geographical gradients in moose body mass.
- III** Garel, M., Solberg, E. J., Sæther, B.-E., **Herfindal, I.** & Høgda, K.-A. (manuscript in press). The length of growing season and adult sex-ratio affect sexual size dimorphism in moose. Ecology.
- IV** **Herfindal, I.**, Sæther, B.-E., Solberg, E. J., Andersen, R. & Høgda, K.-A. (submitted manuscript) Population characteristics predicts responses in moose body mass to temporal variation in the environment.
- V** **Herfindal, I.**, Lund, E., Andersen, R., Solberg, E. J. & Høgda, K.-A. (manuscript) Environmental conditions, body mass and vital rates in a harvested roe deer population.



## Summary

Temporal and spatial variation in the environment can influence the performance of individuals in wild ungulate populations. Of particular importance is an understanding of the mechanisms that shape variation in individual body mass, because several important life history traits are directly related to body mass. Body mass is one of the first traits that is influenced by environmental variation, and often the effect operates through variation in the components of the foraging niche of ungulates. In this thesis, I aim to demonstrate how measurements of environmental variation relate to variation in the foraging niche of ungulates. Furthermore, I aim to explore how variation in ungulate life history traits relates to these variables, and finally, how the management of ungulates could benefit from the incorporation of knowledge about the effects of environmental variation on population dynamics. I use weather observations, large-scale climate indices, and indices of environmental phenology based on satellite-derived vegetation indices (NDVI) to analyse the effect of environmental variation on plants and body mass in moose (*Alces alces*) and roe deer (*Capreolus capreolus*) populations.

The environmental variables that explained most of the variation in plant performance, measured as radial growth in common juniper (*Juniper communis*) also explained variation in ungulate body mass. These variables were related to conditions in spring and early summer. Plant growth was low in cold summers, and in spring where the green-up curve as measured by change in photosynthetic activity during spring was moderate. Such growing conditions are recognised to increase the quality of the plants as forage for ungulates. Consequently, moose body mass in autumn showed the opposite pattern than juniper to environmental conditions, indicating that quality of plants, rather than the quantity, is an important component in temperate ungulate foraging niche. Further, regional variation in moose body mass was associated with environmental variables related to forage quality. Roe deer body mass was associated with availability of forage during winter, and not with factors related to summer conditions. Factors related to forage quantity neither influenced temporal nor spatial variation in body mass in the two species.

Accordingly, it appears that both weather observations and satellite-derived vegetation indices are able to effectively predict variation in plant performance related

to variation in foraging conditions for ungulates. The variation in forage quality in space and time created variation in body mass between populations and between cohorts within a population. Further, the variation in body mass between moose population, caused by variation in the foraging conditions, predicted how the populations differentially respond to the effects of environmental stochasticity. In populations with a high mean body mass, or a low density relative to plant biomass production, available resources buffered environmental stochasticity, and were less influenced by environmental variation than populations with relatively fewer resources available.

If wildlife managers fail to incorporate the effects of environmental variation on population performance, e.g. on the recruitment rate, the population may show unexpected and large fluctuations in size. Therefore, managers should attempt to incorporate knowledge of recent environmental conditions on the population when setting harvesting quotas. In face of the large variation in environmental conditions experienced by the ungulate populations in Norway, and the fact that responses to environmental variation varies between populations, management should be regionally adapted, and aim to incorporate variation in vital rates caused by environmental conditions. This is likely to create more stable and predictable populations.

In face of the predicted climate and landscape changes in Norwegian forests, environmental variables, e.g. from satellite-derived vegetation indices, have the potential to be a powerful tool for a sustainable management of ungulate populations. Consequently, such information should be incorporated into the management of ungulates in order to a) obtain a management of ungulate populations that is adapted to regional mechanisms of environmental variation, and b) acquire a management that is sustainable in face of future change in climate and landscape that may vary regionally. This calls for a regional differentiation in management strategies.

## **Introduction**

### **The foraging niche of temperate ungulates**

Herbivores as a functional group have been claimed to have access to unlimited resources of food (Hairston et al. 1960, Slobodkin et al. 1967). Although this may not be true world-wide, or for all seasons (Polis 1999, Danell & Bergström 2002, Bond 2005), temperate and boreal regions certainly provide huge amounts of plant biomass during summer, and only a small proportion of this is utilised by herbivores (Slobodkin et al. 1967, Polis 1999, Danell & Bergström 2002). Much of the biomass produced in summer is available also during winter as twigs and stem. It has therefore been argued that herbivores are not limited by their food resources, but rather regulated by predators, pathogens or parasites (Slobodkin et al. 1967, Danell & Bergström 2002). However, individual species do not have the same broad diet niche as the functional group they belong to (Hofmann 1989), and the world may not be as green for a species as for a functional group. Still, species of large temperate herbivores (such as moose *Alces alces* and roe deer *Capreolus capreolus*) have broad diets, ranging from herbs, grass and other field-layer species, to twigs and shoots from trees and shrubs (Sæther & Andersen 1990, Andersen & Sæther 1996, Duncan et al. 1998, Shipley et al. 1998, Latham et al. 1999, Illius et al. 2002). The ability to utilise a variety of different plant species is necessary since the abundance of species may vary considerably both in time and space. The abundance of forage is thus closely related to the annual net primary production (ANPP), and determines the quantity of forage available (Polis 1999). However, access to forage may be limited even if food abundance is high, e.g. by snow cover during winter (Sæther & Andersen 1990, Andersen & Sæther 1996).

The value of a plant item as a forage resource is determined by the nutrient content and the digestibility of the item (VanSoest 1994). The nutrient content is often measured as content of crude protein, or the proportion of important nutritional components like nitrogen (N), phosphorus (P) or calcium (Ca), often measured as the ratio between nitrogen and carbon (the N:C-ratio; VanSoest 1994). The digestibility is the actual ability to absorb the nutrients that are present from the plant items, and relates to among other things, the fibre content and the presence of chemical components (mainly plant defences) like tannins or phenols in the plant tissue (VanSoest 1994,

Danell & Bergström 2002). Both the nutrient content and digestibility vary considerably between plant species, and within species it varies between locations, seasons and years (Molvar et al. 1993, VanSoest 1994, Wilmshurst et al. 1995, Fryxell et al. 2005a). Preferences for individual plant species or structures as forage among herbivore species is thus reflected by the digestibility and nutrient content of the plants (Skogland 1980, 1984, White 1983, Allison 1985, Danell et al. 1985, Sæther & Andersen 1990, Bø & Hjeljord 1991, Fryxell 1991, Doucet & Fryxell 1993, McArthur et al. 1993, Owen-Smith 1994, Wilmshurst et al. 1995, Duncan et al. 1998, Danell & Bergström 2002, Illius et al. 2002).

Together, these three components, quantity, quality and accessibility, constitute the foraging niche (in the basic niche concept of Hutchinson 1957) of herbivores. Because these three factors may vary considerably both annually, seasonally, and between habitats, the realised foraging niche experienced by an individual or a population varies correspondingly. Although much of the variation in plant biomass and quality in a given area is explained by soil characteristics (Moen 1999, Polis 1999), a considerable proportion of the spatial variation, and the majority of temporal variation is attributed to climatic conditions, e.g. temperature, moisture and incoming solar radiation (Moen 1999, Polis 1999). These factors are thus able to create spatial and temporal variation in plants that influence one or several of the components of ungulates foraging niche (Skogland 1984, Jonasson et al. 1986, Sæther & Andersen 1990, Bø & Hjeljord 1991, Albon & Langvatn 1992, Andersen & Sæther 1992, Sæther & Heim 1993, Owen-Smith 1994, Sæther et al. 1996, Post & Stenseth 1999, Mysterud et al. 2001a, Pettorelli et al. 2001, Lenart et al. 2002, Olf et al. 2002). The foraging niche of ungulates is therefore a complex composition of three factors that may co-vary or vary independently in time and space (Parker 2003, Fryxell et al. 2005a).

Several studies stress the importance of quality, rather than quantity or accessibility, for foraging behaviour and ecology in temperate and arctic herbivores, particularly during winter (White 1983, Sæther & Andersen 1990, Bø & Hjeljord 1991, Andersen & Sæther 1992, Duncan et al. 1998, Lenart et al. 2002). Of particular importance is the availability of a balanced ratio of nutrients in the diet (Fryxell & Lundberg 1997). The importance of forage quality is further emphasised by evidence that small increases in quality of forage can strongly influence animal performance, e.g.

body mass, through a multiplier effect (White 1983). However, it has proven hard to distinguish between the relative importance of the three components on individual or population performance of wild ungulates (Hanley 1997, Parker 2003). Often, climate indices or weather observations are used as general measures of environmental conditions, but linking climate to the individual components that influence foraging niche is not straightforward. Certainly, the need for data that describe the temporal and spatial variation in foraging conditions for ungulates is evident. Such data should have a high spatial and temporal resolution, cover several years, and have measures that are directly related to ungulate foraging ecology, i.e. the plants and their variation in abundance and quality.

Previously, such data have been hard to acquire. However, lately, several sources of data that meet these requirements have become readily available through vegetation indices derived from satellite-images (Kerr & Ostrovsky 2003, Parker 2003, Pettoirelli et al. 2005). One example is the GIMMS data set (Høgda et al. 2001, Tucker et al. 2001, Zhou et al. 2001). The high temporal resolution (15 days between each image) allows an estimation of several important variables related to plant phenology (Høgda et al. 2001, Pettoirelli et al. 2005). Furthermore, with a spatial resolution of 8x8 km<sup>2</sup>, available since 1982, and measurements that relate directly to plant performance through variation in photosynthetic activity (Reed et al. 1994, Pettoirelli et al. 2005), the GIMMS data offers several new approaches to research on ecological mechanism related to ungulates (Pettoirelli et al. 2005). The recent availability of this information allows the testing of specific hypothesis related to the effects of variation in foraging conditions on ungulates performance. But, in order to do so, one first needs a better understanding of how these variables relate to variation in the components of the foraging niche of ungulates.

### **Foraging niche and body mass in ungulates**

Temperate ungulates often show large intra-specific variation in phenotypic traits, demography and population dynamics, both in time and space (Gaillard et al. 2000). One phenotypic trait of particular interest is body mass. In ungulates, body mass is one of the first traits to be influenced by environmental variation (Sæther 1997, Lindström

1999), and in turn has been repeatedly shown to influence several important life-history traits. For various temperate ungulate species a high body mass is related to high survival (Putman et al. 1996, Loison et al. 1999a, Garrott et al. 2003), high reproduction rates (Sand 1996, Solberg et al. 2002, Stewart et al. 2005), large litter size (Andersen et al. 2000), a longer reproductive period in females (Sæther & Haagenrud 1983, Albon et al. 1987, Langvatn et al. 1996, Sæther et al. 1996, Sand 1996), higher reproductive success in males (Clutton-Brock et al. 1982, Kruuk et al. 1999, Mysterud et al. 2004), and higher future reproductive success of offspring (Albon et al. 1987, Andersen & Linnell 1998, Beckerman et al. 2002, Garrott et al. 2003). Factors that influence body mass thus have influence on both individual and population performance.

Recently, a more thorough understanding of how body mass influences population dynamics has been developed, both theoretically and empirically, using long-term time-series that include both individual measures of body condition and reproductive performance (Gaillard et al. 2003). One important factor emphasised by these studies is the lasting effects of cohort variation in body mass (Loison & Langvatn 1998, Forchhammer et al. 2001, Gaillard et al. 2003, Solberg et al. 2004), which may even last for generations (Beckerman et al. 2003). Such cohort effects arise mainly through variation in environmental conditions at critical stages for growth and development (Beckerman et al. 2003). The life-long performance of this cohort thus depends of the environmental conditions at young ages (Beckerman et al. 2003).

Environmental conditions that affect forage conditions (i.e. the quantity, quality and accessibility of plants) therefore have important effects on traits that shape population dynamics, through their effect on body mass. If one can recognise the environmental factors that, by creating variation in the foraging niche, shape body mass variation, it should be possible to get a better understanding on how variation in the foraging niche space influences important life history traits. Being able to locate a population in the foraging niche makes it possible to further explore the consequences this has for variation in phenotypes. In particular, one can expect variation in vulnerability to environmental stochasticity to differ between populations that are located differently in the foraging niche. If one can predict the response to environmental conditions, it should be possible to adjust the harvest management

according both to the regional phenotypic traits, and according to environmental conditions, so as to counter the predicted changes in population performance.

### **Management of Scandinavian wild ungulates**

Ungulates are intensively managed in Scandinavia (Cederlund et al. 1998, Lavsund et al. 2003). Wildlife managers face several challenges when they set quotas to achieve the desired population sizes. Dense population can cause substantial damage to agricultural crops and forests in early stages (Sæther et al. 1992, Latham et al. 1999, Ward et al. 2004). Furthermore, with high ungulate density, the frequency of traffic collisions increases (Seiler 2005), with high associated socio-economic costs (Sæther et al. 1992, Seiler 2005). On the other side, there are many benefits of ungulates including economic income for landowners by selling hunting permits, recreational opportunities, and their potential as food resources. Modern management aims to balance these considerations.

In Scandinavia, the management of ungulates is mainly done by setting harvesting quotas based on the previous year's harvest or abundance indices based on observation made during the harvest (Cederlund et al. 1998, Solberg et al. 1999, Lavsund et al. 2003). The goal the last decades has been to increase the production, primarily through selective harvest by biasing quotas to calves and adult males, retaining the reproductive part of the population, and consequently increasing the population's potential growth rates (Cederlund et al. 1998, Lavsund et al. 2003). However, this has resulted in skewed age- and sex-structures in many of the populations (Langvatn & Loison 1999, Solberg et al. 2002, 2005), introducing several unwanted side effects related to the skewed sex- and age structures (Mysterud et al. 2002, Solberg et al. 2002, 2005). Despite the attempts of managers who aim for stability, populations have been shown to fluctuate between years. This can partially be due to the fact that environmental conditions that can influence the performance of a population are seldom accounted for in the management system. This has the potential to increase the fluctuation in population size (Haydon & Fryxell 2004). The time-lag in management response to changes can further increase the magnitude of these fluctuations. Therefore, knowledge of how the environment influences the performance of herbivore

populations, both directly through survival and recruitment, or indirectly through body mass variation creating cohort effects, should make it possible to adjust management to be more adapted to environmental variation operating on a local or regional scale.

## **Aims for the thesis**

In this thesis, I aim to search for mechanisms that relate environmental conditions to spatial and temporal variation in vegetation and the performance of wild ungulate populations. Furthermore, I aim to explore if and how the managers of ungulate populations is able to incorporate environmental variation when setting harvesting quotas.

More specifically, the following questions are addressed:

1. How do different indices of environmental conditions relate to plant performance (**paper I**)? Plant performance, e.g. measured as radial growth in perennial woody plants, is influenced by variation in the environment (Linderholm et al. 2003). This can create variation in growth rate between different locations (Linderholm et al. 2003). Furthermore, temporal variation in the environment can generate fluctuations in the plants' suitability as forage for herbivores. The environmental variation can be measured from several sources, e.g. weather observations, large-scale climate-indices, and indices of environmental phenology from remotely sensed images. In order to understand how these variables can influence ungulate populations, we first need knowledge about how variation in plant performance relate to these environmental variables.

2. How does the spatial variation in phenotypes among ungulate populations relate to environmental conditions associated with their foraging niche (**paper II** and **paper III**)? Through the effect on forage plants, variation in the environment can influence ungulate phenotypes, particularly body growth and body mass (Sæther 1997). This can create differences in body mass between populations.

Body mass often shows latitudinal gradients, and several hypotheses exist to explain this pattern. The most important are: A) Winter severity increases with latitude, and this selects for larger body size, either due to a better heat conservation in large individuals (Bergmann's rule, e.g. Ashton et al. 2000) or due to the ability to tolerate

long periods of food shortage during winter (Boyce 1979, Lindstedt & Boyce 1985). B) Population densities influence body mass through intraspecific competition for forage (Stewart et al. 2005). Latitudinal gradients in population densities could then shape gradients in body mass. C) Forage quality increases with latitude (Bliss 1962, Klein 1970), and even small changes in forage quality can have large impact on body growth and development through the multiplier effect (White 1983).

Ungulates often show some degree of sexual size dimorphism (Loison et al. 1999b, Pérez-Barbería et al. 2002). This can be due to faster growth and/or a longer growth period for one sex over the other, most commonly the male in ungulates (Loison et al. 1999b). Variation in factors related to body growth is thus expected to influence the degree of sexual size-dimorphism. This includes variation in foraging conditions, population densities, and variation in reproductive effort in males and females between populations.

3. How does the temporal variation in body mass in ungulates relate to environmental conditions associated with their foraging niche (**paper IV** and **paper V**)? Temporal variation in body mass is expected to be related to temporal variation in foraging conditions, e.g. through variation in quantity or quality of the forage (Sæther et al. 1996, Sæther 1997). However, body mass may also be influenced by population density through intraspecific competition for food (Solberg et al. 2004, Stewart et al. 2005), and by winter conditions influencing loss of body tissue (Reimers 1984, Cederlund et al. 1991).

4. Do population characteristics that are related to the realised foraging niche, influence the susceptibility to environmental stochasticity (**paper IV**)? Variation in the niche-localisation among populations may be visualised through individual performance (Holt & Gomulkiewicz 1997), e.g. in phenotype traits like body mass. Vulnerability to environmental stochasticity may be related to the niche localisation in two respects. A) Individuals that have a niche localisation close to the optimum (e.g. have a higher body mass) are less vulnerable than small individuals since they have a buffer of resources available to meet poor environmental conditions. B) Individuals that have a niche localisation close to the optimum are able to benefit more from favourable conditions than individuals located far from the optimum, and should therefore respond more rapidly to environmental variation. These effects can also be visualised through other

buffers of resources, e.g. through available forage resources measured as population density in relation to available plant biomass.

5. To what degree are managers able to incorporate the effect of environmental conditions on population dynamics in their management of populations (**paper V**)? Often, quotas are based on counts or indices from previous years, or counts during spring prior to the hunt in autumn (Cederlund et al. 1998, Solberg et al. 1999, Lavsund et al. 2003). However, vital rates may vary considerably between years, often as a consequence of environmental variation (Skogland 1984, Grøtan et al. 2005). This can create variation in population size that not are detectable from indices of population size from previous year, or counts prior to the breeding period. If managers are not able to take into account the effect of environmental variation on population dynamics when they set the hunting quotas, population may have unexpected and large fluctuations (Haydon & Fryxell 2004, Fryxell et al. 2005b).

## Methods

### Study species

In order to answer the questions raised in this thesis, I have focused my analysis on four species, two wild and one domesticated ungulates, and one plant.

The moose is the largest ungulate in the Scandinavian forests, with a live adult weight of above 500 kg in males, females being approximately 25 % lighter (Solberg & Sæther 1994, Andersen & Sæther 1996). Moose forage on grasses, herbs, heather and some browsing of deciduous trees like several *Salix* spp., rowan (*Sorbus aucuparia*), aspen (*Populus tremula*) and birch (*Betula pubescens*) during summer (Bø & Hjeljord 1991, Andersen & Sæther 1996), while during winter when snow cover limits the access to plants at the ground layer, the diet switches to browsing of twigs and shoots, preferably deciduous species (Sæther & Andersen 1990, Andersen & Sæther 1996). The rut occurs mainly during late September, early October, but adult females that are not fertilised at the first attempt may have a second ovulation during November (Andersen & Sæther 1996). Calves (one - three, two are most common in multiparous females, Andersen & Sæther 1996) are born at the end of May - start of June (Sæther et al. 1996), and females first ovulate in their second or third autumn, depending on body mass

(Sæther & Haagenrud 1985, Sæther & Heim 1993, Andersen & Sæther 1996, Sand 1996).

The roe deer is the smallest ungulate in Scandinavia, with adult animals of both sexes reaching a live body mass of 30 kg with very limited sexual size dimorphism (Andersen et al. 1998). Their diet consist mainly of herbs during summer (Cederlund & Nyström 1981, Duncan et al. 1998, Latham et al. 1999), while during winter, they switch to more browsing when snow cover limits the access to ground species (Cederlund & Nyström 1981, Holand et al. 1998). Their rut lasts from late July to mid August, and females ovulate only once during this period (Hoffmann et al. 1978), with implantation of the blastocysts delayed by 5 months (Sempéré et al. 1998). One to three fawns are born during May - June (Andersen & Linnell 1997), where litter size is higher for multiparous and heavy females (Andersen et al. 2000).

In Norway, we can separate between wild reindeer (most reindeer populations in southern Norway) and semi-domesticated reindeer (all of northern Norway and some populations in southern Norway; Fauchald et al. 2004), both belonging to the species *Rangifer tarandus*. In this thesis, we only use data from semi-domesticated reindeer populations, and refer to semi-domesticated reindeer only by reindeer henceforth. The reindeer herds are driven between seasonal ranges, following natural migration routes mostly between coastal areas with access to herbs and graminoids in summer and more continental areas with high lichen cover during winter (Fauchald et al. 2004). In autumn, prior to the movement to the winter ranges, a proportion of each age- and sex-class is slaughtered. The live body mass in autumn for reindeer calves is approximately 40 kilograms, but can vary considerably between herds and years, e.g. due to the plant quality on the summer and winter ranges (Fauchald et al. 2004).

Both moose and roe deer are harvested by human hunters throughout Norway. Hunting occurs during autumn (August - December for roe deer, September - October/November for moose), with a break in the moose hunt during the peak of the rut. Harvesting regimes are intended to promote high recruitment rates, and quotas are set for a relatively high harvest of calves and males, and low harvest of reproductive females. Hunting can generate a selection for groups of animals killed, e.g. size-specific harvest mortality (Skogland 1988). However, since both moose and roe deer seldom

operates in flocks during the hunting season, hunters' selection for size is not likely to occur in these species.

Juniper (*Juniperus communis*) is a dioecious plant that has shrub-like morphs in arctic and alpine environments (Høeg 1996). The distribution in Norway covers most of the vegetation regions, from coastal heather to alpine tundra. Radial growth per year is clearly visible as annual rings, and the growth varies considerably between locations and years due to variation in the environments.

## Study area

The study area in **papers II, III and IV** (Fig. 1) includes moose populations covering the range of moose distribution in Norway (Lavsund et al. 2003). The areas are all dominated by forest. The northern areas are mainly in the northern boreal zone (Moen 1999), dominated by birch (*Betula pubescens*) and Scots pine (*Pinus sylvestris*). Further south, Norway spruce (*Picea abies*) dominates and the vegetation zones change to southern boreal, and at the southernmost area, nemoral zone with some broad-leaf tree-species (Moen 1999). Commercial forestry is intensive throughout the whole area. All areas are hilly, with the northernmost areas having the highest elevation ranges. Agricultural areas mainly occur in the bottom of the valleys, and in the central and southernmost areas (Moen 1999), but make up only a small proportion of the land area. In the coastal areas, winters are generally warmer and have more precipitation than the inland areas which have a continental climate, influencing whether precipitation comes as snow or rain during winter. However, the coastal areas in the north still have most of the precipitation during winter as snow.

Finnmark county, from where data used in **paper I** (Fig. 1) was collected, constitutes the northernmost part of the mainland of Norway. The tree-limit here is at 400 - 500 metres above sea level, with a clear coast-inland gradient in the tree-limit exists, with tree-limit being closer to sea-level for the coastal areas (Moen 1999). The topography is hilly at the coastal areas, while the inland is dominated by the large flat Finnmarksvidda plateau. Only a small proportion of the county is used for agricultural purposes.

The island from where the data analysed in **paper V** are collected (Fig. 1) is located in the southern boreal zone (Moen 1999). The island is dominated by a mixture of agriculture areas and mixed forest. The climate is coastal, thus snow-depths are rather low during winter.

## **Data collection**

### **Population data**

Individual data on harvested moose were gathered for the period 1982 - 2002, yielding population specific information on body mass, age, and sex (Solberg et al. 1997). Body mass was measured as carcass mass, which is the mass of the individual minus head, skin, metapodials, bleedable blood and viscera, and constitutes on average 50 % of total body mass (Wallin et al. 1996). Age was determined based on tooth replacement in the lower jawbone for calves and yearlings, and by counting the number of layers in the secondary dentine of the incisor for 2.5 years old and older individuals (Haagenrud 1978, Hamlin et al. 2000). The moose harvest is organised through hunting districts within municipalities, and for analysis one municipality (average size is 875 km<sup>2</sup>) is considered to be one population. The populations cover the range of moose distribution in Norway, from the southern populations inhabiting the boreo-nemoral vegetation zone, to arctic populations in the northern boreal zone (Fig. 1). As indices of population density, the number of moose killed during the harvest in relation to above-ground primary production (from the phenology indices, see below), was used.

Since 1984, individual data on roe deer killed during the annual harvest has been collected from the island of Ytterøya (28 km<sup>2</sup>) in Trondheim fjord (Fig. 1). These data included carcass mass (measured as for moose), age, and sex. Age was determined by tooth replacement pattern in the lower jawbone in fawns and yearlings (Aitken 1975), and from tooth wear patterns based in adults.

The reindeer data is collected through the Ecosystem Finnmark project (Fauchald et al. 2004), where the body mass of slaughtered calves is monitored for each reindeer husbandry annually. In addition, juniper twigs were sampled in 2003 on an area covering the summer ranges of the reindeer herds (Fig. 1). These twigs allowed for measuring the annual radial growth of juniper for each location.

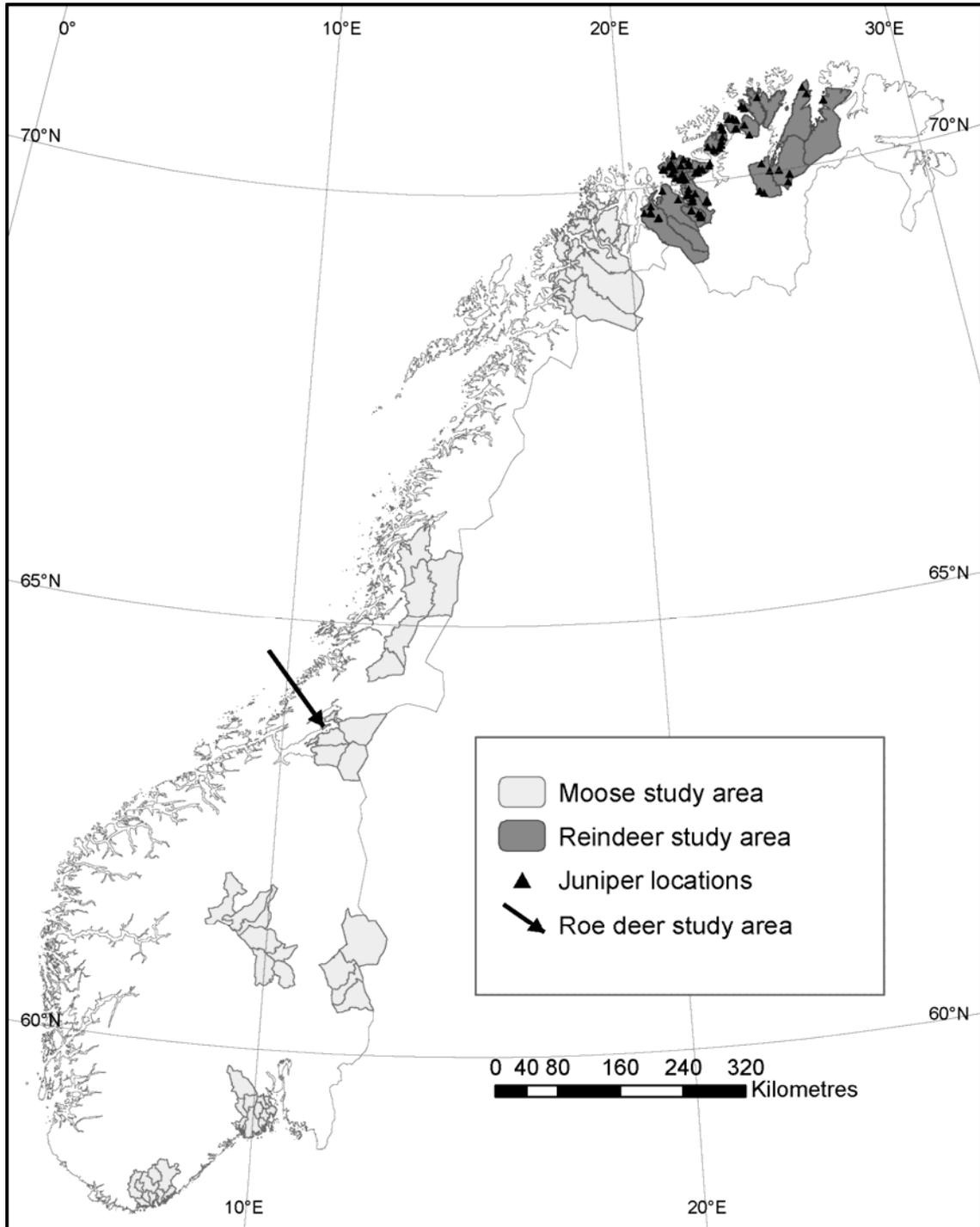


Figure 1. Norway with the populations of moose, roe deer and reindeer, and locations of juniper samples used in this thesis.

### **Climatic data**

For each population (roe deer and moose), climatic data from the closest weather station were collected. For some populations, the distance to closest weather station was rather long (more than 100 km), and I always chose a station within the same climatic zone (e.g. coastal, continental) as the study population. The climatic data included monthly measures of precipitation, temperature and snow cover. The North Atlantic Oscillation (NAO) is a climate phenomenon influencing temperatures and precipitation in the North-Atlantic (Hurrell 1995), and has been widely used in ecological research (Hurrell et al. 2003, Myrsterud et al. 2003a). It is expressed by an index based on the difference of normalised sea level pressures between Lisbon, Portugal, and Stykkisholmur, Iceland, from 1864 through 2004 for the winter period (December - March). A high positive NAO index is generally associated with relatively warm winters with much precipitation in the northern Atlantic coastal Europe, whereas low values of the index tend to result in cold winters with low levels of precipitation (Hurrell 1995). The Arctic Oscillation is closely related to the NAO (Thompson & Wallace 1998), but predicts weather events better at higher latitudes (Thompson & Wallace 1998). The NAO- and AO indices for the study period were retrieved from the web sites <http://www.cgd.ucar.edu/cas/jhurrell/indices.html> (last read 1. June 2005) and <http://horizon.atmos.colostate.edu/ao/> (last read 14. November 2005), respectively.

### **Satellite-derived indices on plant phenology**

The Global Inventory Monitoring and Modelling System (GIMMS) Normalised Difference Vegetation Index (NDVI) dataset is based on satellite images from the Advanced Very High Resolution Radiometer (AVHRR) sensor onboard the afternoon-viewing NOAA-satellite series (Tucker et al. 2001). The GIMMS-data exist in several spatial resolutions, however, for these analyses, the resolution was approximately 8 x 8 km<sup>2</sup>. In order to minimise distortions due to atmospheric conditions (e.g. clouds, haze), 15-days maximum composites were used, together with a median kernel filter, to describe the annual NDVI-curves. NDVI is a vegetation index used as a surrogate for photosynthetic capacity, and measured as (Myneni et al. 1995):

$$\text{NDVI} = (\text{NIR} - \text{RED}) / (\text{NIR} + \text{RED}),$$

Where NIR and RED are the near-infrared and red, respectively, band from the satellite images. The annual curve in the Northern Hemisphere will typically have a very low value during winter, increase rapidly during spring to a high value in early summer, and decrease during autumn (Tucker et al. 1986). The shape of the curve will vary regionally, particularly along a latitudinal gradient (Tucker et al. 1986), like in our study area (Fig. 2b). From the annual phenology curve, eight variables known to be related to plant phenology (Reed et al. 1994, Pettorelli et al. 2005) were calculated (Fig. 2a). Onset of spring (OS) is measured as the week number in spring when NDVI-values reach levels corresponding to leaf burst on birch. Onset of autumn (OA) is the week number in autumn when NDVI-values drop below the corresponding value. Length of growing season (LGS) is then the number of weeks between OS and OA. Peak time (PT) is the week number in summer when NDVI-value reaches its highest level, while Peak value (PV) is the NDVI-value at this time. Length of spring (LOS) is number of weeks between OS and PT. Derived spring NDVI (DSN) is measured as the NDVI-value at OS, minus the NDVI-value at the previous 15-day composite image, and integrated NDVI (IN) is the area below the curve from OS to OA.

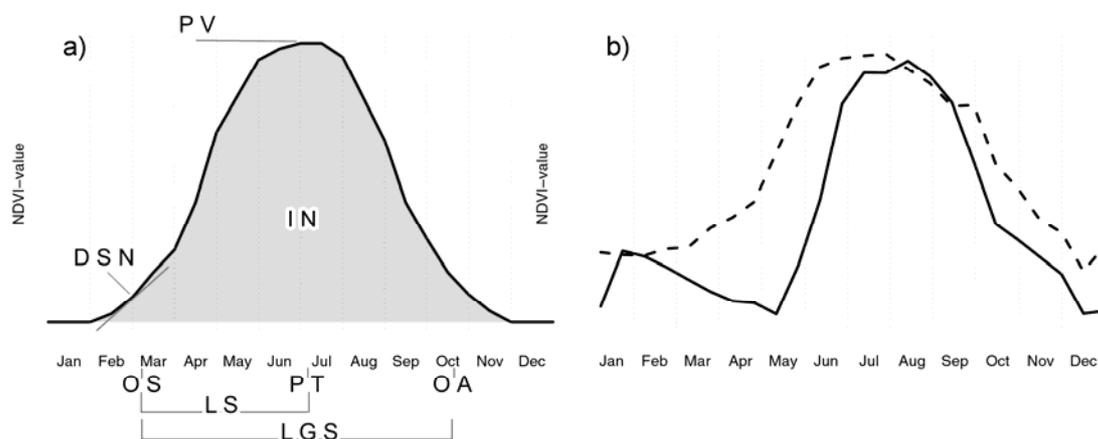


Figure 2. a) A schematic illustration of the phenological indices derived from the annual NDVI-curve. b) The annual phenology curve from the northernmost (solid line) and southernmost (dashed line) moose populations (Fig. 1). Abbreviations: OS = onset of spring, OA = onset of autumn, PT = peak time, LS = length of spring, LGS = length of growing season, DSN = derived spring NDVI, IN = integrated NDVI, PV = peak value.

The phenology indices can relate to several variables important for the value of plants as forage for herbivores (Reed et al. 1994, Veroustraete et al. 1996, Boelman et

al. 2003, Dong et al. 2003, Wang et al. 2004a, b). Most important is probably 1) onset of spring determines how early herbivores can start feeding on high-quality forage after the winter, 2) onset of autumn indicate when high-quality forage is no longer available, and 3) length of growing season indicates for how long a period high-quality forage is available. Moreover, 4) peak time indicates when photosynthetic activity reach its highest level, and plant quality (particularly N:C-ratio) is known to decrease after this, 5) the peak value indicates how much foliage is available at the maximum, while 6) the length of spring indicates for how a long period high-quality forage is available, where a long spring provides high-quality forage for a longer period than a short spring. Finally, 7) derived spring NDVI reflects the rate of greenness development during spring, while 8) integrated NDVI is considered as a measure of foliage biomass production during the growing season.

## **Statistical procedures**

For all comparisons between the environmental conditions, including the climatic variables, the satellite derived phenology indices, and body mass, we used linear models, accounting for age and sex where relevant. Although such relationships have shown non-linear relationships in some studies (Mysterud et al. 2001b), we did not consider our sample size (counted as number of populations or number of years for a population) to be of sufficient size to account for non-linearity. In addition, visual inspection of our data plots did not indicate any obvious non-linear patterns.

As the data regarding moose and roe deer were obtain from hunter harvest, there was considerable variation in the kill date. The body mass of cervids may vary considerably through length of an autumn hunting season, e.g. calves and yearlings grow heavier, while adult males often lose body mass during the rut (Miquelle 1990, Solberg et al. 2004). This variation may affect the estimation of mean annual body mass, and to account for this, carcass weights were adjusted by regional estimates of change in body mass during hunting season for each age and sex-class (**paper II, III and V**). Body mass measures for populations were averaged for each age- and sex-class, for each year. Furthermore, for the analyses concerning geographical gradients in body mass (**paper II**), the means of all annual values for each population were used. In

**paper III**, the adjusted carcass mass were used to fit sex-specific growth curves for each population to estimate adult body size, the decay rate, and the time of active body growth.

With known age of the harvested individuals, one can reconstruct the minimum number of individuals alive in a specific year, if the data have been collected long enough to allow several cohorts to pass completely through the population, assuming that the hunting effort and age-specific hunting vulnerability are relatively stable from year to year (Fryxell et al. 1988, 1991, Solberg et al. 1999, 2004). As the age of the roe deer killed during hunt at Ytterøya was known for a sufficient number of years, the population was reconstructed and its density, growth-rate and adult sex ratio calculated annually based on the reconstruction.

To remove any influence of location-specific macroclimate and temporal autocorrelation in the time series of **paper I and IV**, first-order differentials were extracted from standardised growth for each juniper location, and body mass from reindeer and moose populations (Chatfield 1989).

## **Results and discussion**

### **Question 1**

How do different indices of environmental conditions relate to plant performance?

The radial growth of juniper was positively related to i) summers that were warm and with little precipitation, ii) spring with a steep plant development progression, and iii) low snow-depths in April. Thus, several of the indices of environmental conditions were able to explain the variation in plant performance. This included both weather observations and indices derived from satellite images. Plant growth seems to depend on the length of periods with high temperatures (Chapin et al. 1995, Arft et al. 1999, Linderholm et al. 2003). During years with warm and sunny spring and summers, plants have more resources available for growth, whereas access to water not seems limiting for plant growth at this latitude, a common observation in coastal temperate regions (Linderholm et al. 2003). The higher growth in warm summers is likely to decrease the proportion of nutrients in the tissues, and make the plants less suitable as forage (Deinum 1984, Bø & Hjeljord 1991, Chapin et al. 1995, Lenart et al. 2002).

Juniper is not selected as forage by Scandinavian ungulates (Andersen & Sæther 1996, Duncan et al. 1998, Skogland 1994, Gebert & Verheuden-Tixier 2001), and variation in growth is thus likely to not be influenced by variation in ungulate density. Since several studies indicate that plants at least within a functional group and within vegetation zones respond in a similar manner to variation in the environment (Kellomäki & Kolström 1994, Chapin et al. 1995, Arft et al. 1999, Post & Stenseth 1999, Lenart et al. 2002), juniper growth may be a good indicator of variation in environmental conditions that affect ungulates.

The importance of plant growth rate on the quality of the plants was reflected by the negative correlation between juniper growth and autumn body mass of reindeer calves that grazed in the study area during summer. Accordingly, the sources of environmental conditions, and in particular those that relate to spring and early summer, are able to predict variation in the components of the foraging niche of ungulates. Thus, environmental variables originating both from weather observations and from satellite-derived vegetation indices, reflects foraging conditions for ungulates. These measurements provide a tool for investigating the effect of temporal and spatial variation in forage conditions on ungulate populations.

## **Question 2**

How does the spatial variation in phenotypes between ungulate populations relate to environmental conditions associated with their foraging niche?

Mean body mass varied considerably among Norwegian moose populations, and showed a very clear latitudinal trend with higher body mass in the north. No single environmental variable gave a better fit of the body mass variation between populations than latitude, but a variable describing the shape of the environmental phenology curve came closest. According to this variable, higher body mass was found in areas that had a late onset of spring, a short and intense summer, a relatively early onset of autumn, and accordingly a long winter. This supports two hypotheses regarding the latitudinal gradient in body mass.

Firstly, forage quality of plants in general increases with latitude as a result of the plants adaptation to the short summers with long days (Bliss 1962, Klein 1970).

These growing conditions force the plants to allocate resources to growth and reproduction, rather than anti-herbivore mechanisms, e.g. chemical components (Bliss 1962). This will then benefit the herbivores, and can explain the latitudinal gradient in body size reported for several species (red deer *Cervus elaphus*; Langvatn & Albon 1986, roe deer; Andersen et al. 1998, moose; Sand et al. 1995). Accordingly, moose at higher latitudes benefit from higher quality of forage during summer, and possibly also during winter. This can generate large effects on body mass through the multiplier effect (White 1983).

Secondly, in harsh environments, mortality during winter can be size-dependent, i.e. mortality increases with decreasing body mass (Lindstedt & Boyce 1985). This selects for faster growth, since individuals that grow fast during summer and autumn have higher survival during winter. However, as non-human related moose mortality in general is low during winter in Norway (Sæther et al. 1996, Stubsjøen et al. 2000) and seems unaffected by latitude (Sæther et al. 1996, Stubsjøen et al. 2000), this selection seems to be of minor importance in our study populations at present. However, the selection pressure for large sizes may have been higher in northern Norway than in southern Norway in the past, creating the gradients in body mass that we observe today. Accordingly, the present latitudinal gradients in body mass can relate to their ability to tolerate long periods of fasting. As both the forage quality and the fasting tolerance hypotheses seems likely, and are not mutually exclusive, we suggest both to be likely in shaping the latitudinal gradient in moose body mass in Norway.

A multiple model with several of the environmental variables included achieved a better fit than latitude alone. The effect of environmental phenology on body mass variation was also strong in this model, even when accounting for latitude, suggesting that this variable follows other gradients than the latitudinal gradient alone. Accordingly, several climate gradients may generate body mass differences. This includes coast-inland gradients, altitude-gradients or gradients in population densities. Thus, the results are in accordance with several studies on body mass variation in moose: it increases with latitude, and decreases with increasing population density, altitude and decreasing winter severity (e.g. Sand et al. 1995, Sæther et al. 1996, Hjeljord & Histøl 1999, Ericsson et al. 2002, Solberg et al. 2004). This suggests that variation in body mass between Norwegian moose populations are shaped firstly on a

latitudinal gradient in environmental phenology influencing plant quality and selection for fasting tolerance, and secondly along other ecological gradients including coast-inland, altitude or population density.

There were considerable difference in the growth patterns of males and female moose. Males grow faster and for a longer time than females, and this difference between the sexes varied between populations. Most apparent was the effect of the length of the growing season of plants, i.e. the period between onset of spring and onset of autumn. Populations that experienced short growing seasons had higher sexual size-dimorphism than populations that experienced long growing seasons. This was probably a result of the higher forage quality of plants that have limited time for development through the summer. Accordingly, the quality of forage influences how fast the moose grow, and as females start reproduction at an earlier stage than males, the males benefit from forage quality in terms of body mass for a longer period, increasing the sexual size dimorphism.

In addition, populations with a highly female-biased sex-ratio had a low sexual size-dimorphism. This most likely relates to at what age the males enter the reproductive stage. Since reproductive success is related to both age and size in male moose (Andersen & Sæther 1996), the best strategy when competing for females is to grow large before starting the reproduction (Andersson 1994). This may not be the situation if there is less competition for females due to a female-biased sex-ratio (Mysterud et al. 2003b, Mysterud et al. 2004). Accordingly, the males allocate energy to rutting and reproduction activity at an earlier stage in highly female-biased populations (Mysterud et al. 2003b, Mysterud 2004), and sexual size-dimorphism decreases.

### **Question 3**

How does the temporal variation in body mass in ungulates relate to environmental conditions associated with their foraging niche?

Like the variation in body mass between moose populations, annual variation in body mass within populations was also high. The body mass in autumn was positively related to plant growing season that started early, had a slow plant development in spring, lasted long, and to cold summers. These factors are related to high quality of

plants as forage, but negatively to the biomass as measured as net primary production (Deinum 1984, Bø & Hjeljord 1991, Lenart et al. 2002). Thus, the annual variation in moose body mass is most likely shaped by variation in forage quality, rather than quantity, during summer. This confirms earlier results regarding the importance of forage quality in the diet of moose both during summer (Bø & Hjeljord 1991, Sæther & Heim 1993, Sæther et al. 1996) and winter (Sæther & Andersen 1990, Shipley et al. 1998).

In the roe deer population, however, the body mass in autumn was not associated with summer conditions. Rather, high body mass was related to low snow-depth the previous winter. In addition, harsh winter conditions seemed to negatively influence recruitment rates. As a very selective feeder (Latham et al. 1999), the roe deer may have the ability to acquire sufficient amount of high-quality forage during summer despite varying summer conditions. This may particularly be true in the heterogeneous landscape on Ytterøya, with large areas of mixed agricultural and forested areas. However, being less adapted to tolerate Scandinavian winters than the moose (Holand et al. 1998), snow cover during winter may to a higher degree limit the accessibility to forage, and increase the energetic expenditure related to movement (Holand et al. 1998). This also influenced recruitment rates, possibly through increased rates of implantation failure (Hewison & Gaillard 2001) or stillbirths (Andersen & Linnell 1998). Accordingly, roe deer populations at the latitudinal limits of their distribution may be most vulnerable to winter conditions (Grøtan et al. 2005).

#### **Question 4**

How do population characteristics that are related to the realised foraging niche, influence how susceptible the population is to environmental stochasticity?

Moose populations with high mean body mass showed a lower response to environmental variability compared to populations of small-sized individuals. The same pattern existed between low- and high-density populations, where populations with high density relative to the available plant biomass were more susceptible to environmental variation. Not only did the effect of several environmental variables increase with decreasing mean population body mass and increasing population density, the

percentage of variation in body mass explained by environmental variables was higher for populations with small individuals or high density, compared to populations with larger-sized individuals or with low density. Although several mechanisms may account for this, the results suggest that individuals that have access to a buffer of resources are less vulnerable to severe climatic events (Skogland 1983, Hallett et al. 2004). This buffer of resources may be stored as either body tissue (fat deposits) or be available as forage (low population density and intraspecific competition). The climatic events causing temporal body mass variation can be related to both winter conditions influencing the utilisation of important body tissue, and forage quality in summer important for restoration of body mass, growth, and development. A lack of a buffer of resources thus creates patterns in vulnerability to environmental stochasticity that follow gradients in the distance between the realised and optimum foraging niche, and gradients in population densities relative to the available plant biomass.

### **Question 5**

To what degree are managers able to incorporate the effect of environmental conditions on population dynamics in their management of populations?

Both body mass and recruitment rates in the roe deer population at Ytterøya were influenced by winter conditions. The variation in recruitment rates influenced the growth rate of the population. However, the harvest of fawns was set to be 50% of the total harvesting quotas, even if the proportion of fawns in the population varied considerably between years. Accordingly, the take-off of fawns was too high in years with low recruitment, i.e. if winter conditions were harsh. Thus, the harvest had a strong effect on the population dynamics, indicated by the lack of density effect on growth rate, the lack of response in population size to growth rate, and that population size was highly correlated with harvest the previous year. This suggests that the harvesting regime currently used at Ytterøya does not seem to adaptively account for variation in the vital rates, in particularly the recruitment rates, that occur as a consequence of variation in the environment. A more precise prediction of recruitment, or a monitoring of juvenile population size prior to hunt, and adjusting the take-off of fawns according

to the recruitment, is expected to reduce population fluctuations (Haydon & Fryxell 2004).

## **Future prospects**

This thesis shows that environmental variables can be a good tool for predicting variation in traits among and within ungulate populations, and that variation in these traits can have consequences for the population dynamics, and thereby also for a sustainable management of the species. The future management should attempt not only to maximise production, but also to obtain populations that have age- and sex-structures that allows mechanisms of sexual selection, to occur. This can be important for the viability of the populations (Viken 2005). Finally, it is important to minimise the negative effects of ungulate populations, e.g. damage to forest plantation and traffic accidents.

Satellite-derived vegetation indices, together with weather observations, is today perhaps the most appropriate measures for environmental variation in Norwegian forest ecosystems. These ecosystems will inevitably experience change in the future. This is both due to predicted global climate change (McCarthy et al. 2001, Saxe et al. 2001), but also through a change in succession stages of the standing forest. Forestry is possibly the factor that influences forage availability for ungulates most in Norwegian forests.

Both these sources of change are detectable with readily accessible data. More important will be to predict how the Norwegian forests appear in the future. Climate change can change the species composition (Sætersdal et al. 1998), as well as the value of species as forage for herbivores (Lenart et al. 2002). Similarly, succession of forest stands leads to changes both in quantity and quality of forage (Sæther et al. 1992), causing a change in the carrying capacity of an area. Since the magnitude and impact of changes from both climate and landscape is likely to vary regionally (Høgda et al. 2001, McCarthy et al. 2001), and since populations of ungulates do not necessarily respond to variation in the environment in the same manner, the management of ungulates should be spatially differentiated both according to the present landscape, expected future changes, and to population characteristics.

New programmes of satellite imagery provides data of higher quality, making it possible to obtain even more information about the quality of the landscape, e.g. through the MODIS-programme (Hansen et al. 2002, Myneni et al. 2002). A goal for the future must be to incorporate such information into management of ungulates, together with better knowledge about the relationships between the environment and variation in population dynamics, in order to obtain sustainable management of healthy ungulate populations.

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