

Natural and farmed habitat as a basis for production of red deer in Norway

PROJECT TEAM

Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biology, University of Oslo. Prof. Atle Mysterud (Project leader), Dr. Leif Egil Loe, Ph.D. student Vebjørn Veiberg. The Norwegian Forest Owner Association (Norges Skogeierforbund; NSF). Vidar Holthe. Deer committee Sør-Trøndelag (Hjorteviltregion 2 i Sør-Trøndelag; Hjort S-T). Ivar Syrstad. Deer committee Sunnfjord and ytre Sogn (Sunnfjord og ytre Sogn hjorteutval; Hjort SyS). Hallvard Flatjord

COLLABORATORS

The Norwegian Farmer's Union (Norges Bondelag; NB). Ola Håvard Hoen and Cesilie Aurbakken. Department of Economics (DoE), Norwegian University of Science and Technology, NTNU. Prof. Anders Skonhoft. Museum of Natural History and Archaeology (MoNH), Section of Natural History, NTNU. Dr. Gunnar Austrheim. Telemark University College (HiT). Chief engineer Arne Hjeltnes. Norwegian Institute for Agricultural and Environmental Research (Bioforsk). Researcher Erling L. Meisingset. Hedmark University College (HH). Ph.D. student Barbara Zimmermann. Norwegian Institute for Nature Research (NINA). Senior researcher Rolf Langvatn. University of Lyon, Division of Biometry and Evolutionary Biology, France (ULyon). Dr CNRS Jean-Michel Gaillard, Ph.D. student Bram van Moorter. University of Glasgow, Division of Environmental and Evolutionary Biology, UK (UGlasgow). Dr Dan T. Haydon

Summary

The project will provide a basis to predict the potential for production of red deer based on detailed knowledge of the natural and farmed habitat as well as detailed studies of red deer habitat use in multiple areas. The yield of red deer reached 27600 in 2005. Red deer thus constitute the 2nd most important game species (in meat value), and the one with the fastest increase in yield. The potential income from red deer hunting is therefore increasing, particularly along the west coast. Here, landowners have their main income (on the farm) from livestock and to some extent forestry. Due to recent decreased income from livestock, it has been suggested to develop hunting of red deer as an important addition to more traditional land use. We know that red deer damage agricultural pastures, but not how much red deer use farmed habitat relative to different types of natural habitat and how this affects production parameters of the deer (total number of deer, body weights and calving rates). Due to migration, management often comes short in preventing substantial biases between the red deer related costs and benefits experienced among landowners. Similar problems of cost-benefit distribution have been explored in detail for moose. We aim to use these results to parameterize a bioeconomical model to also be valid for the challenges faced by the red deer management, thereby providing the potential for changing farming practises and going for red deer hunting as a livelihood. Funding from the user side to mark red deer with GPS collars along the west coast is already granted. Deer production data is available from NINA. We currently lack relevant habitat maps to be linked to the red deer GPS- and production data. The expertise of making such maps exists at HiT, the practical skills of marking deer is held by the user side, while the skills of analysing the red deer data exist at UiO together with their international collaborators. The economic part will be done in collaboration with economists at the NTNU. This part will include optimality modelling as well as a questionnaire to investigate how important red deer is to the economy of landowners today, to identify niches in the market. We believe that this project will provide essential knowledge on the potential for production of red deer in traditional farmland areas – in particular along the west coast where other good alternatives are scarce.

PART 1: R&D – The project

1. Aims of the project

The overall aim of the project is to provide knowledge of the role of both the natural and farmed habitat as a factor in production of red deer in Norway. We aim at bringing farming, forestry and hunting interests together with ecological and economic research in order to provide a baseline for how to optimally manage red deer as a rural resource. We will

1. Collect spatial deer data and develop detailed habitat maps to quantify how much time the red deer spend on pastures and natural habitats of different types relative to what is available at various temporal (hour, daily, seasonal) and spatial scales (regions, home ranges), and how much this depends on landscape context (like topography). Thereafter we will assess how different types of pastures and natural habitat types (and their combinations) feed back on production of red deer (body weights and offspring mass; individual level and population level) and in turn red deer numbers. These findings will help us to – at the landscape level – identify areas suitable for deer production.
2. Quantify the grazing pressure in the natural habitat to determine sustainability of the current grazing regime (Gloppen and Flora, Sogn og Fjordane). In particular, how does grazing pressure depend on distance to agricultural pastures, i.e., are natural habitat types close to pastures more intensively used (so-called “neighbourhood effects”; relevant for forestry damage)?
3. To find out how large areas each individual deer use and to find the proportion of migrating individuals. This will be used to evaluate if the landowners paying the cost of deer damage in winter and spring, are the same as those profiting from deer hunting during autumn. Thereafter, we will gather data on the various cost and income components of red deer hunting. Based on the estimated costs and benefits, we will formulate a bioeconomic (dynamic) model analysing both the effect of migration and the vegetation-deer interaction. This will provide suggestions for how to distribute the profit from deer hunting more evenly among landowners. We will also do a questionnaire of how important red deer is to the economy of landowners today to identify niches in the market.

2. State of the art

The agricultural system of Norway has been based on extensive use of outlying pastures of fairly low productivity compared with much of Europe. The use of these areas peaked around 1860-1880, when an estimated 2.9 million sheep, 0.4 mill. goats and also cattle each summer were free ranging (Drabløs 1997), and there was an intense summer farming in the mountains (Kvamme 1988; Moe et al. 1988). Economic changes then led to a much lower level of use around 1910, with increases mainly in sheep number after this time. With a growing industry now providing N-fertilization, and the general industrialization of agriculture, the (winter) fodder for livestock could be produced much more efficiently on small areas around the farms. This made use of outlying pastures less important, in particular for cattle where new, larger breeds took over. A combination of reduced use of upland summer pastures (involving extensive logging of firewood) and climate change have resulted in a quite dramatic altitudinal increase in the timberline (Hofgaard 2001). In addition, extensive planting of spruce in the 1950's and the following decades has changed the mainly deciduous habitat along the west coast. All of these coarse scale land use changes, in addition to the introduction of selective harvesting in the early 1970's, resulted in a dramatic increase in red deer numbers along the west coast, partly taking over grazing resources previously used by livestock (Ahlén 1965; Ahlén 1975; Mysterud et al. 2002).

The population size of the Norwegian red deer is today historically high. While the annual harvest in the 1960's was between 2-3000 deer, the yield reached 27600 in 2005; increasing in recent years with more than a 1000 deer annually (Statistics Norway). Red deer thus constitute the 2nd most

important game species in terms of meat value (after moose), and the one with the currently fastest increase in yield. The agricultural system of Norway is still changing quite rapidly. While the economy in livestock husbandry (such as sheep farming) is decreasing, the potential income from red deer hunting is increasing, particularly along the west coast where most of the red deer are shot (Figure 1). Landowners in this area have traditionally had – and still have - their main income (on the farm) from livestock (maintained on forage from pastures) and to some extent forestry. The potential for using red deer hunting as a part of rural livelihood has not been evaluated. This seems like a better option than farming red deer, due to high costs of infrastructure such as fences in the topographically steep terrain along the west coast of Norway.

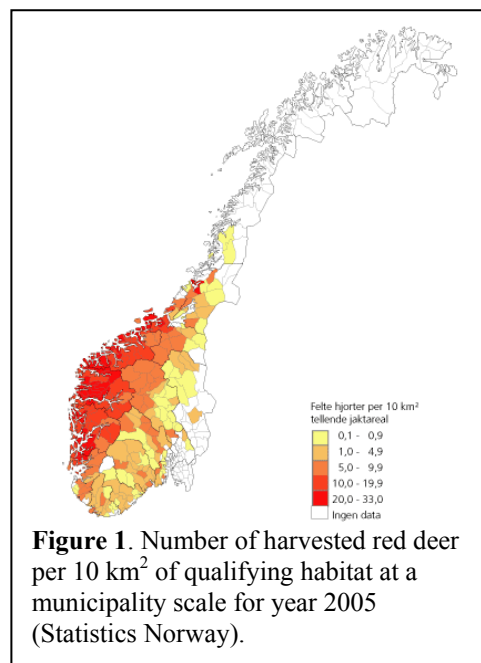
Even though high red deer densities might have the potential for economic profit, these high densities also give

rise to two general types of conflicts to other management goals; those directly related to economic costs and those related to ecological issues (cfr. challenges below). All over the world ungulates come in conflict with traffic arteries (e.g., Groot Bruinderink and Hazebroek 1996), and red deer in Norway is no exception (Myserud 2004). Collisions with red deer often result in the death or severe injury of the animal and a dented vehicle and sometimes injured people. The mean socio-economic cost of one moose-car collision is estimated to 162 000 to 210 000 NOK (Vegdirektoratet). In addition, the landowner loses a prospective gain of a potential hunting object, and also the national community loses due to payment of insurances. In addition, red deer may locally damage agricultural crops at the west coast of Norway (Meisingset et al. 1997), removing as much as 50% of the grass production (Meisingset and Krogstad 2000). The loss again strikes the landowner. In addition to depleting agricultural crops, red deer may also harm the forest. Red deer damages to forestry are mainly caused by bark stripping of spruce and young pine stands during winter. Fungus and other microorganisms infecting wounded trees cause rapid timber quality reduction resulting in reduced income for the landowner when stands are cut (Veiberg and Pettersen 2000; Veiberg 2000; Veiberg and Solheim 2000). Moreover, reduced recruitment of deciduous forest have also been registered as a consequence of red deer browsing (for Scotland: see Milner et al. 2002). Landowners experiencing considerable crop or forest damages may experience a substantial economic loss. The fact that these costs as well as the gain from the red deer hunting varies considerably among areas and landowners, represent a major challenge to the local wildlife management. Disagreement and disputes regarding management goals, as well as distribution of benefits and compensation of costs related to the red deer, is often nourished by the lack of knowledge and conflicting interests. Increasing the understanding of deer space use and how they utilize farmed and natural habitat types will help to improve the red deer management and subsequently reduce the level of conflicts related to it.

3. The challenges

3.1 Landscape level potential for red deer production

Assessing the link between habitat/plant productivity and red deer productivity is difficult, and can be done both at an individual and population level. Though one clearly can measure plant productivity in each habitat directly, deer use of resources in a landscape is typically much more complex, being very much influenced by topography and other local factors in a landscape context (e.g., Senft et al. 1987; Lima and Zollner 1996). Simple habitat productivity maps are therefore not likely to yield the relevant information required, though some kind of habitat map seems essential. We need both spatially explicit habitat maps as well as detailed data on how red deer use these



habitats at different spatial (regional, within seasonal home ranges) and temporal (feeding bout, daily, seasonal) scales. There is a high number of methods to measure habitat selection (e.g., Thomas and Taylor 1990). A very promising way of establishing a spatially explicit map of potential deer productivity, is to spatially link deer use to a large number of habitat components with Resource Selection Function's (RSF's; Box 1).

With such RSF tools, we can predict red deer productivity at coarse scales. We aim to use the extensive database of red deer body weights (>60000 deer) covering the main distribution range of red deer along the west coast. We have extensive experience in using these data at a coarse, municipality scale (e.g., Mysterud et al. 2001a; Mysterud et al. 2001b; Mysterud et al. 2002). Most focus has been on variation related to age, density and climate. At present, the spatial analyses have been limited in part by inadequate habitat maps (Mysterud et al. 2002). With the improved habitat maps, coupled with the RSF's, we will be able to analyse habitat specific variation in red deer productivity.

Access to farmland can be seen as valuable habitat enrichment in much of the Norwegian red deer populations' distribution area (Mysterud et al. 2002). While the use of farmland is typically pooled in such habitat analysis, we aim at identifying the most important stage of the pasture to red deer, and how the level of exploitation vary between seasons, individuals and populations. Increased knowledge about habitat preferences will lead to better understanding of habitat requirements. Such insight can be a valuable tool for the wildlife management, when actions are taken either to improve marginal red deer habitats, or when the management aim at reducing conflicts concerning distribution of costs and benefits related to a common red deer population.

3.2 Sustainable grazing levels in natural habitats and the role of farmland

Large ungulates are among the most important species determining vegetation composition and diversity of many other organisms (e.g., Hobbs 1996; Côté et al. 2004). The dense populations of red deer has led to concern among managers that the habitat may have become overgrazed (Punsvik 2002); i.e., that the intense grazing has reduced coverage of preferred food plants over time (cfr. Mysterud 2006). We do know that the huge increase in the red deer population has resulted in reduced individual growth (Mysterud et al. 2001c), which has reduced winter survival of calves (Loison and Langvatn 1998; Loison et al. 1999) and delayed age of first reproduction (Langvatn et al. 2004). However, these measurable density dependent reductions in red deer productivity (e.g., 10% fewer yearlings ovulate; Langvatn et al. 2004) are fairly small compared to the observed effects in for example moose populations (Solberg et al. 2006). An equally interesting question is thus why density dependent effects are not stronger? It may be that the extensive use of farmland by red deer, which is fertilized and renewed regularly, may dampen the density dependence. This can have two impacts on the use of natural habitat; either a reduction of the grazing pressure or, more likely, a more severe overgrazing of natural habitat, since access to farmland may lead to increased density of red deer. This relationship will likely vary with season and the regional deer density. Small scale studies suggests that red deer may indeed have negative impact on plant production and invertebrate activity (Melis et al. 2006). Most important from the perspective of deer management and productivity, is how much red deer affect their own preferred feeding plants at coarser, management scales. This is an important issue to address, because when encouraging to test out hunting of red deer as an addition to the traditional livelihood, we need to know if this livelihood really depends on sustaining the current livelihood (such as a continued renewal of pastures). Providing knowledge about which type of agricultural pastures are preferred, one might consider attracting red deer by presenting the type of pastures preferred by the deer. Before doing this, we need to examine at relevant, coarse management scale, how the use of important *natural* forage species (such as bilberry and rowan; Ahlén 1965) is affected by distance to agricultural pastures, and if the observed grazing levels of *natural* forage species are sustainable. From a red deer perspective this is important since they provide the most important forage for deer in mid-winter.

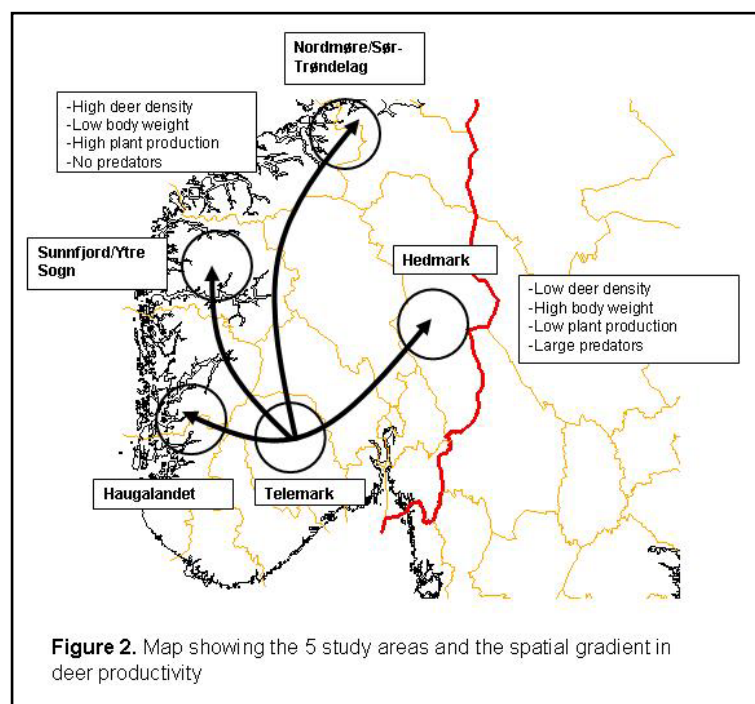
3.3 Scale of management and cost-benefit distribution

An important concern when it comes to distribution of costs-benefits related to red deer, is the fact that most ungulate populations in the temperate zone migrate between separate summer and winter ranges (e.g., Histøl and Hjeljord 1993; Mysterud 1999). There is currently only one available study quantifying this for red deer, and this was done in Snillfjord, Sør-Trøndelag, at the northern border of the distribution range (Albon and Langvatn 1992). We know that red deer is migratory, but little about how large part of the population that migrates, which factors that affect the timing of migration and the distance covered, and what characterises summer and winter habitats. Such information has important implications in securing sustainable wildlife management and if aiming for a livelihood based on red deer hunting related income. This has been very important for moose management, but it remains to be determined if this is equally clear-cut in red deer. In particular, the very long distance migration found for red deer in Snillfjord (Albon and Langvatn 1992) is unlikely representative for red deer further south, due to a very different topography. Therefore, to characterise migration of red deer in multiple areas along the west coast is needed to find appropriate scales for management.

Two challenges regarding management of red deer are related to the severe damages red deer can cause on commercial forestry (e.g., Gill 1990; Veiberg and Pettersen 2000; Vospernik 2006), and damages on the agricultural production (Meisingset & Krokstad 2000). Damage to forestry is mainly a problem on red deer wintering grounds. Costs of damages related to grazing of pasture and damages to other agriculture productions, may on the other hand occur during most of the vegetative growing season and in both summer and wintering areas as well as along migration routes. The income (i.e., harvesting) is typically in summer/autumn ranges where the red deer often stay until the latter part of the hunting season. When population management comes short in preventing substantial biases between the red deer related costs and benefits experienced among landowners, alternative distribution models need to be found. Similar problems of cost-benefit distribution has been explored in quite some detail for moose (Skonhoft and Olaussen 2005; Skonhoft 2005), and one of the project aims is to expand these models to also be valid for the challenges faced by the red deer management. Based on the data to be collected within this project, it will be possible to determine over how large scales landowners should aim to collaborate to provide a fair distribution of resources. Can this be solved within municipalities? Or, as for moose, do we need collaboration across these administrative boundaries? Cfr. Box 2 for the bioeconomic approach to be used.

4. Methods

To achieve our aims we will collect new high-resolution spatial data on a large number of female red deer in different parts of Norway (Figure 2). We will make detailed vegetation maps of farmed and natural habitat types covering the same areas to assess the importance of these vegetation types for deer use. Existing and new data on deer numbers, carcass weights and reproduction will be implemented to investigate how farmed and natural habitat feed back on production of deer (Aim 1). Thereafter we will combine this approach with a field census to assess sustainability of key



natural forage species and along pasture-natural habitat gradients to look at neighbourhood effects from pasture (Aim 2). Finally (Aim 3), we will parameterize a bioeconomical model with collected data on positive and negative effects from deer production, which in turn may lead to detection of areas where a stronger focus on deer production might be economically beneficial. Each aim will through the study period result in minimum 1 scientific paper in high quality peer-reviewed journals.

To achieve **Aim 1** we need detailed spatial data on red deer use and a vegetation map. We will collect **data on deer spatial distribution** by GPS-collaring female red deer. Through the course of the study we will mark 65 female deer in Sunnfjord/Ytre Sogn (some already marked), 180 deer in Nordmøre and Sør-Trøndelag and 10 females in Hedmark with Tellus Basic GPS-collars (Televilt, Sweden). Local veterinaries will be responsible for the marking activity, which will take place on established winter feeding sites in the time period December to April. Animals are darted with a CO₂-injection rifle and immobilized by a mixture of ketamine and medetomidine. This method and the drugs have already been thoroughly tested. Along with marking, measures on body size and weight will also be recorded. All collars are fitted with a drop-off mechanism enabling the collar to be released from distance. Each GPS-logger has the capacity to collect up to 20 000 positions during one year where 95% of them are accurate to the closest 5 meters. In addition we have access to already existing data in Hedmark (11 females), Rogaland and Hordaland (Haugalandet; 22 females) and Telemark (14 females). We will make **high-resolution vegetation maps** covering the central areas where we have red deer fitted with GPS-collars by covering 60x120 km in Sogn & Fjordane, a similarly sized area on Nordmøre/Sør-Trøndelag and 60x60 km areas in Haugalandet and in Hedmark. We will map habitat by use of high-resolution satellite images (SPOT5) together with aerial photos (orthophotos), digital maps (N50) and extensive field calibration. Habitat maps based on satellite photos are often criticised for being too coarse scaled and unreliable and therefore of little value. We overcome this in two ways 1) by using satellite photos with 9 times higher resolution than normally used (10 x 10 m instead of 30 x 30 m squares which is the normal resolution in LANDSAT pictures) and by acquiring “ground truth data” in the field. Analytically, we will use a object-based classification approach in a GIS environment (Burrough and McDonnell 2000), more specifically a directed nearest neighbour classification using a Fuzzy set approach (Burrough and McDonnell 2000; Hjeltnes 2006) in the software eCognition (Definiens Imaging). With this method we will get the following information 1) dominating and sub-dominating tree species 2) openness in the tree-layer, 3) dominance of heather, grass and herbs in the field layer, 4) type and biomass of pasture and 5) occurrence of impediment. A pilot study using this method has already been conducted in Telemark (by a collaborator in this study) with very promising results (Hjeltnes 2006). To further assess the quality of pastures we will investigate if the age of the pasture (since renewed) and species composition is important for deer’s selection of pastures. After red deer GPS-data is retrieved we will identify the home range of each individual deer. Within this home range we will randomly select a number of pastures. Based on local knowledge in each municipality (partners in this project) we will identify each landowner and ask him to provide information on the above mentioned parameters.

The vegetation map will be matched with a variety of spatial data related to deer production. **Deer body weights** have been provided by hunters since 1991 (available from Rolf Langvatn, NINA, a partner in the project). The number of **observed deer per unit hunting time** has also been reported by hunters in selected areas (available from Erling L. Meisingset, Bioforsk). **Calf production** can be estimated from ovulation rates (Rolf Langvatn, NINA) and also from the proportion of adult females seen with a calf. At the level of the municipality we will estimate if the proportion of different natural and farmed habitats is important for body weights and pregnancy rates. To investigate the same question on the **individual level**, we aim at shooting females marked with GPS-collars close to the end of the normal hunting season (15th November). Then we will have the unique situation where we know the exact habitat selection of each individual in the past year and can directly assess how this translates into production (body weight change since catching and

if it calved or not). We have deer data available from a larger area than where we will develop vegetation maps. In addition we will therefore through the course of this study initiate collaboration with Norut (through Senior researcher Bernt Johansen). They will by August 2007 have a course scaled (30x30 m) LANDSAT-based vegetation map covering all of Norway. Firstly, this opens up for a comparison between our fine-grained, detailed vegetation map and the more coarse grained LANDSAT-based map in overlapping areas. Secondly, if found adequate in this comparison, we will relate the full set of population level data (deer numbers, body mass etc) to the LANDSAT-based vegetation map.

When we have accurate GPS data from red deer, an accurate vegetation map of both natural and farmed habitat, together with the data base on deer production measures, we will apply statistical methods given below (Box 1) to fulfil Aim 1.

Box 1. Statistical analyses

Resource Selection Functions (RSF's) (Manly et al. 1993; Boyce and McDonald 1999; Manly 2002). At the individual level we will use RSF's to relate the spatial red deer data to habitat characteristics. To account for individual variation we fit each individual as a random factor in the RSF (Gillies et al. 2006). RSF's uses a multivariate approach which is ideal when relating deer use to multilayered GIS maps. For our use this implies that we can simultaneously assess the importance of various habitat types (including pastures), altitude, slope and aspect, all factors that we have reason to believe is important for individual deer's selection of site (Mysterud et al. 2001a).

$$\tau(\mathbf{x}) = \exp(\beta_0 + \beta_1x_1 + \beta_2x_2 + \dots + \beta_kx_k) / [1 + \exp(\beta_0 + \beta_1x_1 + \beta_2x_2 + \dots + \beta_kx_k)] \quad \text{Eqn 1}$$

Statistically speaking, we will fit a logistic model, $t(\mathbf{x})$, to the independent variables where the dependent data are one for used units and zero for available but unused units: The selection coefficients, β_i , in the log-linear model are estimated by the logistic regression coefficients (Eqn 1). We simply use the numerator, $w(\mathbf{x})$, to distribute the use of resources across the landscape (Boyce and McDonald 1999; Manly 2002). We will use RSF's to spatially link habitat characteristics to the potential for deer production as follows: 1) to link both use and selection (i.e., use relative to availability) of both vegetation types and other factors such as altitude, slope and aspect. 2) the outcome of this analyses will be used to parameterise a model on a landscape scale extrapolating the likely potential for red deer production in different areas. Clearly, this is a form of extrapolation and there are clear limitations to how far one should use RSF models from one area. It is vital to have a data from the various regions of red deer, which we aim to cover with this proposal.

Generalized Linear Models (GLM; McCullagh and Nelder 1989). At the population level we will use GLM's to investigate if various habitat characteristics (at the spatial scale of municipalities) feed back on 1) red deer numbers ("seen deer" data collected by hunters), 2) the number of deer harvested (hunting statistics; Statistics Norway 2006), 3) body weights and 4) ovulation rates (from the NINA monitoring program). At the individual level we will use Linear Mixed-Effects Models (Pinheiro and Bates 2000) and Generalized Additive Models (GAM's; Woods 2006) to relate body weight and presence of offspring to the same habitat variables. Here we will in addition account for (and quantify) individual variation by including each individual red deer as a random factor in the analyses. All statistical analyses will be performed with the software R (R Development Core Team 2006).

To achieve **Aim 2** we will perform **field measures of the grazing pressure** in natural habitat types with increasing distance to pastures. We aim to determine the spatial variation in grazing pressure on natural winter forage plants of red deer, in particular if distance to agricultural habitat is a key variable. To quantify the level of grazing pressure in natural habitats, we aim to perform altitudinal transects within a block-wise randomization design in focal municipalities in Sogn og Fjordane. Within the assigned blocks, each block representing a part of the municipality, we will choose a random 1x1 km² square, and then do a transect following the altitudinal gradient, from the lowest point (often towards a fiord, farmland or valley bottom) and as high as it is possible to walk/climb. Along the transects, we take samples at random distances of 20-50 m between plots. Each plot is a circle of 4 m in radii. Within each plot we count the proportion of grazed key winter forage species. We will typically focus both on highly selected species such as bilberry and rowan, but also on somewhat lower quality forage. Grazing on low quality forage will indicate a more severe grazing pressure (cfr. Mysterud 2006). We will also investigate if the relative use of natural habitat types

change with increasing distance from pastures by combining data from the GPS marked red deer and the vegetation map (see above). The statistical approach of doing this is given in box 1.

Box 2. Linking ecology and economy: a bioeconomic modelling approach

Based on available estimates of economic costs (agricultural damage) as well as ecological data sampled in the municipality of Gloppen, we aim to formulate a bioeconomic model analysing the role of migration and the vegetation-red deer interaction and through simulation determine the optimal deer density and winter grazing pressure in their natural habitat. Through such a model the costs of reaching specific 'sustainable' red deer density levels may be quantified. See Clark (1990) for a general overview of bioeconomic modelling, while Zivin et al. (2000), Swanson (1994), Swallow (1990), Huffaker et al. (1992), Brown (2000) and Skonhøft (1999) all are examples of applications of this framework on the ecology-economic interactions of terrestrial animal species.

The model will be formulated in discrete time with seasonal subdivision between the summer season (Milner-Gulland et al. 2004) and winter season. The red deer population will be structured as reproducing (≥ 2 yr) and non-reproducing (juvenile and yearlings) (e.g., Caswell 2001, Gaillard et al. 1998, see also Skonhøft et al. 2002). Detailed demographic data on red deer are available (e.g., Myrseth et al. 2001b; Myrseth et al. 2001c; Langvatn et al. 2004; an age structured Leslie-matrix population model is available from Langvatn and Loison 1999). Natural mortality takes place during the winter (Loison and Langvatn 1998; Langvatn and Loison 1999; Loison et al. 1999; Veiberg and Solheim 2000). The production (weight growth) is related both to the winter climate (the North Atlantic Oscillations, NAO, Myrseth et al. 2001b) and temperature in May affecting spring plant phenology (Pettorelli et al. 2005), which may be determined within the model.

The vegetation growth is influenced by the grazing pressure as well (Crawley et al. 2004). The plant-herbivore interaction is therefore dynamic (Noy-Meir 1975; Bayliss and Choquenot 2002); the stocking level and grazing pressure one year influence the vegetation growth determining the red deer biomass growth next season, and so forth. For obvious reasons, the cost structure differs between the summer and winter seasons (see above). Due to the dynamic nature of the plant-herbivore interaction, the planning problem itself is dynamic. When assuming that the management goal at the landowner level is to maximise the present-value landowner profit, the problem of finding the efficient stocking size and grazing pressure may be formulated within an optimal control, or dynamic programming, framework (e.g., Kennedy 1986; Conrad and Clark 1987; Clark 1990). The control variable is the yearly offtake. The solution at the landowner level will next be contrasted to what happens when adding the *in-situ* value of the red deer habitat; that is, the present-value social cost is maximised (the social planner solution in the economic jargon). The landowner level costs of reaching specific (sustainable) red deer density levels may then be quantified. This plant-herbivore model may typically be calibrated for a standardized landowner size with its accompanying amount of red deer habitat, or for a fixed amount of outfield area, say 1 km². The ecologic as well as economic data collected will be scaled to such levels.

To achieve **Aim 3** we will estimate the size and overlap of winter and summer kernel home ranges (HR; Worton 1989) as well as migration distances between core winter and summer areas. Based on a set minimum distance and lack of overlap between seasonal HR we will estimate the proportion of migrating deer in each of the five investigated populations. We will relate the size and distance between summer and winter HR to the distribution of property sizes, to investigate how many landowners typically "share" a deer in the various seasons. Thereafter, we will gather data on the various cost and income components of red deer hunting, and the various indirect income effects in the study areas. This includes meat value (NOK/kg) and the estimated loss in kg body weight at increasing deer densities (i.e., density-dependent body weight reduction). The primary direct cost will be the loss of crops from pastures. Season-dependent quantifications of the actual costs have already been conducted (Bioforsk, Fureneset), from whom we will access published data to be able to parameterize the bioeconomic model (cfr. Box 2). We will parameterize two models, one to optimize total amount of meat (kg), and the other to optimize total number of harvested deer, since the value of one deer will differ based on which of these currencies are chosen. A number of biological and social factors may determine whether it is feasible to provide products to hunters in the market. We will perform a questionnaire of how important red deer is to the economy of landowners today to identify niches in the market so as to understand better the options and constraints to develop this further (Box 3).

Box 3. Current status and potential for development of red deer hunting as a rural livelihood

Only a limited number of studies have explored the importance of big game hunting as a component of rural landowner livelihood, and they are all focussing on moose (Johansson et al. 1988; Sødal 1988; Mattsson 1990a; Mattsson 1990b; Mattsson 1994; Sylvén 1995; Storaas et al. 2001; Horne and Petajisto 2003). The value of hunting may change over time relative to other primary resources managed by the landowners, as a consequence of trends in population size of deer, national economy and regional policy. As the red deer population has increased over the past decades, a growing proportion of landowners along the west coast of Norway now offers various products related to red deer hunting. Income related to such products has become an important part of the household economy for many rural landowners. However, documentation concerning product diversity, potential improvements and the actual extent of this contribution to rural economy is limited. This part of the project aims to improve our knowledge about the different niches in the market, and the landowners' perceptions of red deer as a potential source of income on their property. Already now, we can identify at least 3 strategies; (1 - "intensive preparations") exclusive, guided hunting aiming mainly for large trophies and mainly in the best hunting areas, (2 - "moderate preparations"), less exclusive, recreational hunting aiming for all categories of animals, with some guiding and often short hunting periods, and (3 - "minimum effort"), just renting out the hunting right of a property and a cabin for a longer hunting period.

Our investigation will be based on a questionnaire among landowners regarding the role of red deer hunting in their current economy. The details of the questionnaire will be developed together with the user group. Some aspects we aim to answer are: What are the actual costs and benefits of providing hunting permits under different strategies? Both average investment costs, fixed costs and running costs of landowners providing different products will be revealed and this information may serve as useful information to landowners when they decide which product to present to the market. Furthermore, we need to identify why landowners select the different strategies. Do they base their choice on physical differences in terms of the size of their land, the size of the red deer quota, the abundance of potential trophy males, if they have a cabin or other accommodation available for rent, their financial opportunity to invest, the time horizon in their planning, other sources of income, how large the present share of their income originates from hunting, if the landowner himself hunts, what the neighbours do with their land or their evaluation of red deer damage on agricultural pasture? Or is there also a social pressure to avoid foreign hunters?

Professor Anders Skonhøft (NTNU) will be responsible for this part, while the actual survey and analysis will be performed by Jon Olaf Olaussen, NTNU. Olaussen is supervised by Skonhøft and will defend his PhD thesis in March 2007 on the economy in river-salmon fishing. He has therefore a very good background to perform such a questionnaire. Two months of salary (mid-March to mid-May 2007) and postage will be carried through the existing budget. Since we cannot cover the full range along the west coast, this part of the project will include Norges skogeierforbund (NSF) members in Sogn og Fjordane only. To allow a wider survey including Rogaland/Hordaland with 1360 NSF members; Møre og Romsdal with 2260 members, and more sophisticated analysis, we will apply Skogtiltaksfondet for additional funding. Indeed, it is important with careful analysis to control for potential bias arising from variable return rates of the questionnaire. Generally, the more comprehensive the questionnaire is, the lower is the response rate. A low response rate means that it is difficult to assess the generality of the results. There may be non-response bias, meaning for example that a distinctive type of landowners may not return the questionnaire. Therefore, it is important with at least one reminder (preferably two or three) to improve the response rate. The backing from the NSF will increase the likelihood of receiving a high number of responses. We are welcome to use their member lists (and get for free stickers with addresses), which will facilitate this part greatly.

5. Project organisation

The project leader, Prof Atle Myrseter, is in the core group of Centre for Ecological and Evolutionary Synthesis (CEES, recently awarded status as a Centre of Excellence), UiO and holds a considerable expertise in wildlife biology, analysis of a wide variety of ecological data (from grazing to population dynamics) and as a project leader of multidisciplinary research teams, including work with economist Anders Skonhøft (Nilsen et al. 2007) and grazing researcher and botanist Gunnar Austrheim (e.g., Myrseter and Austrheim 2005; Evju et al. 2006). Atle Myrseter has worked intensively with the ecology of the Norwegian red deer the last decade – resulting in both status as Outstanding Young Investigator (OYI/YFF) awarded by the Research Council of Norway and receiving the Nansen award for young scientists in 2005 from the Academy of Sciences and Letters (see CV). Other project members at UiO have knowledge on GIS and deer-collar programming. The Norwegian Forest Owner Association (Norges Skogeierforbund; NSF,

represented by Vidar Holthe) has members nationwide and is a natural choice of partner in a project with a large geographical distribution (Hedmark, Telemark, and the west coast from Rogaland to Sør-Trøndelag) and where the study species – the red deer – locally have a significant impact on the growth and regeneration of economically important tree species (in particular spruce). The local user organisations, the deer committee in Sør-Trøndelag (Hjorteviltregion 2 i Sør Trøndelag; Hjort S-T) and the deer committee in Sunnfjord and ytre Sogn (Sunnfjord & ytre Sogn hjorteutval; Hjort SyS), represent the local users which have raised the majority of the user-based funding. They will be executive in preparing winter feeding sites prior to marking, the actual marking and retrieval of the GPS-collars in field. The constellation of the administrative team is ideal because of the mixture of national landowner interests in general (NSF) and regional deer management specialists (Hjort S-T & Hjort SyS). As a collaborator, we also have the other nationwide landowner organisation - The Norwegian Farmer's Union (Norges Bondelag; NB). A team of highly qualified collaborators who will do executive tasks has been put together: HiT has the knowledge of making vegetation maps, Bioforsk has expert knowledge on deer management and deer-induced pasture and forest damage, HH has expertise on GPS-collars and has existing spatial deer data, NINA is providing data on deer production in each municipality.

6. International Co-operation

Questions related to management of abundant deer populations and conflict with resources is not unique to Norway. Numerous scientists and managers around the world have eagerly taken the chance to learn more about deer space use by using GPS technology. A few of these scientists have made recent advances in how to model spatial data with respect to habitat use. We have included two leading scientists within this field as collaborating partners; Dr. J-M. Gaillard (Lyon, France) and Dr. Dan T. Haydon (Glasgow, UK). Dr. Haydon is currently involved in the project "Modelling movement of elk using GPS data", working with very similar data sets as the ones to be generated in our project. Together they can advice and help us on finding the optimal analytical tools as well as give fruitful advices based on their experience with different species in different management regimes. In a scientific perspective the project will likely benefit from their presence by leading to at least one comparative scientific paper (comparing their and our data). The project leader has for several years had extensive collaboration with the group of Gaillard and several other leading international groups in ungulate ecology.

7. Progress plan with milestones

Each year the project will run from December to November with the first winter field season being in Møre & Romsdal, Sogn & Fjordane and Hedmark. The second winter field season will take place in Møre & Romsdal and Sogn & Fjordane, while from 2009 marking will only take place in Møre & Romsdal. Summer field work will consist of vegetation mapping starting in Hedmark and Sogn & Fjordane in 2007, before continuing in Møre & Romsdal, Sør-Trøndelag and Haugalandet, in 2008. The milestones for each year are:

- Mark, collar and weigh 40-60 individual female red deer in December to April each year (apart from last year devoted to analyses).
- March-September. Begin mapping and analyses of last year data.
- June-August. Field work related to vegetation mapping.
- November. Process biopsy material sent in by hunters in all involved municipalities (jaws, ovaries, body weights).
- December. Refurbish collars and prepare for next field season.
- November-Following March. Mapping and analyses of summer data.

In addition we have the following milestones:

1. March 2007, apply for more funding for expanding the questionnaire to broader areas along the west coast. In June 2007 complete the questionnaire in Sogn og Fjordane (Box 3), or, if more funding is obtained, December 2007 in a larger area.

ES 419290: Production of red deer in Norway

2. September 2007. 2 master theses on home range, migration patterns and large scale habitat use in red deer will be completed.
3. December 2008. One master thesis on foraging intensity of deer along a pasture – natural habitat gradient will be completed and one scientific paper and one popular scientific article (in Norwegian) will be submitted.
4. Two more master theses and minimum one more scientific paper will be written in the time period 2009-2010.
5. During the study period we will aim at writing one article in the newspaper Nationen, update a web site regularly, and give multiple annual talks in user fora on the progress of the project. In addition we will attend a large annual deer management conference. We will focus strongly on informing landowner and deer management interests orally and in written reports throughout the study period.
6. Following the end of the final field season, completion of analysis, writing up and submission of articles for publication will be achieved by December 2011.

8. Costs for each partner (in 1000 NOK)

Partner	2007	2008	2009	2010	2011	Sum	
NSF	Operational costs	20	20	20	20	100	
Hjort SyS	GPS equipment and annual renewal	167	17			184	
	Deer catching and field work	262	50			312	
	Work and fodder from landowners	166	88			254	
	Administration	225				225	
Hjort S-T	GPS equipment and annual renewal	513	515	132	281	81	1522
	Deer catching and field work	230	210	240	240	240	1160
	Work and fodder from landowners	150	150	150	150	150	750
	Administration	225					225
HH	GPS equipment and annual renewal	23					23
	New GPS deer collars	300					300
	Tracking, travels, diet	26	15	5			46
	Deer fodder	20					20
	Deer catching and field work	20					20
	Administration	12	22	17			51
	Salaries	178	187	43			408
HiT	Vegetation mapping	750	750	0			1500
Bioforsk	Salary researcher Erling Meisingset (incl overhead)	777	563	563	414	169	2486
	Salary technical personnel	200	200	200	180	220	1000
NTNU	Salary Anders Skonhøft (incl overhead)				100	100	200
	Salary Jon Olaf Olaussen (incl overhead)	108					
NINA	Red deer monitoring program	820					820
UiO	Salary Dr. Leif Egil Loe (incl overhead)	684	776	807	839	873	4041
	Salary Dr. Vebjørn Veiberg (incl overhead)			807			807
	Atle Mysterud (5% per year)	62	56	78	78	63	337
	Master students	200		100	100		400
	Group meetings (travels and diet)	30	30	30	30	30	150
	Other operating costs	194	200	200	200	200	1040
	Final report					80	80
Total costs		6362	3849	3392	2632	2226	18460

* 80% of the value of GPS equipment bought prior to the project. This reused equipment is essential for the project

** A part of the user funding was planned in the period 2006-2010. The start of the project will be in 2007 so all this funding has consequently been moved to 2007-2011.

9. Financing (in 1000 NOK)

Partner	2007	2008	2009	2010	2011	Sum
Hjort SyS	BU-funding	200	200			400
	S&F county (Fylkesmannen)	50	50			100
	wildlife fund 11 municipalities	457	170			627
	Own resources landowners S&F	88	88			176
	GPS equipment*	320				320
Hjort S-T	M&R county (Fylkesmannen)	70	70	70	70	350
	S-T county (Fylkesmannen)	50	70	70	70	330
	wildlife fund 15 municipalities	945	445	445	445	2280
	Aasgard landowner comettee	35				35
	Own resources municipalities	300	300	300	300	1500
	Own resources landowners ST & MR	150	150	150	150	750
HH	Hedmark county (Fylkesmannen)	30	20	10		60
	wildlife fund 8 municipalities Hm	105	65	55		225
	Own resources landowners	65	64			129
	Skogeigarlaget Vest	5	5			10
	wildlife fund 10 municipalities R&H	50	50			100
	Hordaland county (Fylkesmannen)	10	10			20
	Rogaland county (Fylkesmannen)	10	10			20
	Vegvesenet	4				4
Bioforsk	Own resources	50	50	50	50	250
NINA	Red deer monitoring program	820				820
UiO	4 master students	200		100	100	400
	Atle Mysterud (~5% per year)	62	56	78	78	337
User funding total		4076	1873	1328	1263	703
Applying from NFR		1829	1581	1651	1095	1219
Applying from DN*		457	395	413	274	1843
Sum		6362	3849	3392	2632	18460

* The formal deadline for applications to DN is 15. January. However, DN is very positive towards the application, and we have an agreement to put their part in the budget with the numbers as given here.

PART 2: Use of results**10. Main idea**

The main idea is to prepare the ground for a better use of the red deer as a rural resource. We will collect all the types of data needed to build a bio-economical model. This implies that we must understand the space use of deer throughout the year (who gets the profit during hunting season and who pays the cost of damage in winter and spring). Since both natural and farmed landscape types are heavily fragmented, the second premise for success is to derive sufficiently detailed vegetation maps. We will acquire spatial knowledge on the profit from hunting resembled by variation in number and weight of harvested animals. All our approaches will be spatially explicit and we will work along a deer production gradient from Hedmark (where the red deer is a marginal resource and prone to wolf predation), via Telemark, to the high density red deer areas on the west coast (Rogaland to Sør-Trøndelag).

11. Innovation

The innovative aspect of this project is to ask the question if it is profitable to reduce the dependency on the century-old traditions of livestock production and instead manage the pastures in a way that favours red deer production. This project may contribute to a mental change from regarding the red deer primarily as a recreational hunting object to an important economical resource. Keeping in mind the decline in profitability from livestock together with the 10-fold increase in red deer harvest the last few decades, our question is innovative and topical for optimal resource use in rural areas. This will have high relevance nationally both in areas where the red deer is already abundant and for future perspectives in more recently colonized areas. In a grander

perspective, we might compare the situation in Norway with other European countries. In Scotland, there is a *cost* of shooting female red deer as hunting is mainly for trophies (males) and the meat is not valued. To avoid such a scenario in Norway we must think ahead when it comes to land use practices, recruitment of hunters and deer management.

12. Use of the results in our organizations

The Norwegian Forest Owner Association (NSF) and The Norwegian Farmer's Union (NB)

- a) *Business idea*: To increase the profitability of natural and farmed habitats by investigating the potential for deer production in different parts of Norway. In some areas this may contribute to reduce the negative trend in income from livestock husbandry. In the long run this may secure the incomes and jobs of members of the organisations.
- b) *Innovation*: To implement the use of a “new” resource in addition to more traditional forest and farmland use. The quantification of deer use of natural and farmed habitats and how this feed back on deer production measures are essential insight to determine the potential for deer production. These findings will certainly be regionally important (on the west coast) and will likely have transferable value to other national and international landowners who want to optimize the use of wildlife resources.
- c) *Economic value for the company*. Our findings may have business economical consequences (i.e., consequences for single landowners in NSF and NB). We will perform a questionnaire among NSF members in Sogn og Fjordane regarding the role of red deer hunting in their current economy. This will help us to improve our knowledge about the investment costs and profit of the different hunting products presented to the market (the products 1-3 in box 3 above). Individual landowners living in these areas may consequently be inspired to change their livelihood more towards deer production. When combined with results from space and habitat use of the deer, we can identify areas and combinations of habitat types (also outside the study area) where a change in land use practices towards deer production could be profitable.
- d) *Realisation*: The members of NSF and NB are interested in sustainable production of agricultural crops, forests and deer and how to optimise and compromise the production of these three components. We will investigate how intensively deer use agricultural areas (i.e., loss of crop) and if there is increased browsing of trees (i.e., forest damage) in the neighbourhood of deer pastures. We will also quantify the potential for economic profit of deer. Each landowner will thereby get advice on how to best realise his natural resources.
- e) *Risks*: The worst case scenario is that we will not reach a conclusion (answer yes or no) on whether there is potential for increased deer production. We have taken precautions to avoid this situation – first by collecting new data of high quality and quantity and second by putting together a team of collaborators with the best premises to fulfil the task. Even if we do not find an increased potential for deer production in Norway the project will generate new management and scientific knowledge.

Deer committees in Sør-Trøndelag (Hjort S-T) and Sunnfjord and ytre Sogn (Hjort SyS)

- a) *Business idea*: To increase the income from red deer hunting and to assess if the distribution of costs and benefits from keeping red deer at high densities are locally democratic; that is to assess if it is the same landowners who pay for the crop- and forest damages as the ones benefiting from hunting.
- b) *Innovation*: The cultural landscapes are currently changing, and many old pastures may no longer be maintained the same way. This may lead to gradual changes in the production of red deer populations. Landowners no longer maintaining their pastures saves these costs but a may also simultaneously experience a loss in the income from red deer hunting. On the other hand, being the only local landowner maintaining high-quality pastures may attract a large number of deer which may severely increase the level of damage. However, this may be compensated for if disproportionately many deer remain on your land during hunting season. We will track the space use of deer to answer how rapidly they respond to local changes in land use.

c) *Economic value for the company.* First, we will investigate which combination of habitat factors (pastures and natural habitat types) lead to highest yield in terms of meat and number of deer. If a landowner could harvest 5 more deer per year this would lead to a conservative increase in income of 20 000 NOK (4000 NOK per deer in meat or hunting value). Secondly, we will quantify the potential profit in different hunting products with increasing levels of investments (box 3). Others (Bioforsk, Furneset) have investigated the actual crop loss to deer and we will access this published information.

d) *Realisation:* Each landowner pays a fee for every big game shot. This significant income is both collected and administered by each municipality. We will identify prevailing migratory routes within and across municipality borders. Our findings will indicate if there should be a regional collaboration in the use of this money instead of just focusing on projects within municipalities.

e) *Risks:* The greatest risk is failure to obtain an adequate sample size. This may be due to failure to capture animals (if deer in mild winters do not visit feeding sites) and/or loss of the costly GPS-collars (granted by the user side in the project) that will be fitted to red deer. However, preliminary tests of this equipment are promising.

13. Consequences for the environment

1. Cultural landscapes are valued for their beauty and history both from residents and tourists. This landscape type, obviously, requires active cultivation by farmers. For many small-scaled livestock farmers the profit is marginal and many quit farming with the consequences of rapid re-growth of cultural landscapes. If we find in this study that maintenance of pastures to red deer production is cost-effective this might represent important incentives for future maintenance of cultural landscapes.
2. Large herbivores such as red deer are often termed landscape architects implying that they are important factors in shaping their living area. We will quantify if the use of natural forage plants (such as blueberry and rowan) is sustainable. Many landowners haunted by deer-induced pasture and forage damages wish to reduce the deer population. Our findings will provide information on whether the red deer population densities experienced today entail measurable ecological consequences for the botanical production and biodiversity.
3. After identifying key habitat traits for deer use we will (based on the vegetation map) develop a map for managers highlighting the most suitable deer areas (for activities such as summer feeding, winter feeding, hiding and migration). This information could be implemented in area planning (such as development of new infrastructure) at the municipal level and in long-term red deer management plans.

14. Other benefits

1. Students from UiO will be involved in the project and earn their Masters degree during the course of the study.
2. As a collaborative partner UiO will gain by subsidizing two young researchers (5 years and 1 year respectively) which will increase their chances of later finding a permanent job in academia.

15. Information and dissemination of results

We will put the strongest effort on multiple oral and written presentations to deer managers and landowners on the progress of the project throughout the study period. We will write articles in popular scientific (such as Hjorteviltet) and hunting magazines (such as Jakt og Fiske and Jeger, Hund og Våpen). Indeed, the project leader has already written numerous such articles (see CV) and will continue to do so also in this project. He is frequently asked to give project updates on management related research on national conferences often gathering 50-100 managers. This will continue to take place minimum once per year throughout the project period. We believe that such fora are ideal for implementing our findings into management decisions. One of our collaborators, Erling L. Meisingset (Bioforsk), will also fill an important role here since he has extensive contacts with the user side and have already held more than 800 talks related to red deer management. In the

end of the project we will write a report in Norwegian aiming at managers at the end of the project. Finally, each aim will lead to one or more scientific papers in peer-reviewed journals and parts of the results will also be presented in the form of Master theses from the University of Oslo.

16. References

- Ahlén I (1965) Studies on the red deer, *Cervus elaphus* L., in Scandinavia. *Swed Wildl Res* 3:177-376
- Ahlén I (1975) Winter habitats of moose and deer in relation to land use in Scandinavia. *Swed Wildl Res* 9:45-192
- Albon SD, Langvatn R (1992) Plant phenology and the benefits of migration in a temperate ungulate. *Oikos* 65:502-513
- Bayliss P, Choquenot D (2002) The numerical response: rate of increase and food limitation in herbivores and predators. *Philosophical Transactions of the Royal Society of London* 357:1233-1248
- Boyce MS, McDonald LL (1999) Relating populations to habitats using resource selection functions. *Trends Ecol Evol* 14:268-272
- Brown G (2000) Renewable natural resource management and use without markets. *Journal of Economic Literature* 37:875-914
- Burrough PA, McDonnell RA (2000) Principles of geographical information systems. Oxford University Press, Oxford
- Caswell H (2001) Matrix population models. Sinauer Associated Inc., Sunderland, Ma.
- Clark CW (1990) Mathematical bioeconomics: the optimal management of renewable resources. Wiley, New York
- Conrad J, Clark CW (1987) Natural resource economics. Cambridge University Press, Cambridge
- Côté SD, Rooney TP, Trembley J-P, Dussault C, Waller DM (2004) Ecological impacts of deer overabundance. *Ann Rev Ecol Syst* 35:113-147
- Crawley MJ, Albon SD, Bazely DR, Milner JM, Pilkington JG, Tuke AL (2004) Vegetation and sheep population dynamics. In: Clutton-Brock TH, Pemberton JM (eds) *Soay sheep: Dynamics and selection in an island population*. Cambridge University Press, Cambridge, pp 89-112
- Drabløs D (1997) The story of the Norwegian sheep. Anniversary review of the Norwegian Sheep and Goat Breeders 1947-1997. Norwegian Sheep and Goat Breeders, Oslo
- Evju M, Mysterud A, Austrheim G, Økland RH (2006) Selecting herb species and traits as indicators of sheep grazing pressure in a Norwegian alpine habitat. *Ecoscience* in press:
- Gaillard J-M, Festa-Bianchet M, Yoccoz NG (1998) Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends Ecol Evol* 13:58-63
- Gill R (1990) Monitoring the status of European and North American cervids. The Global Environment Monitoring System Information Series No. 8, United Nations Environment Programme, Nairobi
- Gillies CS, Hebblewhite M, Nielsen SE, Krawchuk MA, Aldridge CL, Frair JL, Saher DJ, Stevens CE, Jerde CL (2006) Application of random effects to the study of resource selection by animals. *J Anim Ecol* 75:887-898
- Groot Bruinderink GWTA, Hazebroek E (1996) Ungulate traffic collisions in Europe. *Cons Biol* 10:1059-1067
- Histøl T, Hjeljord O (1993) Winter feeding strategies of migrating and nonmigrating moose. *Can J Zool* 71:1421-1428
- Hjeltnes A (2006) Kartlegging av habitater til hjort i deler av 4 kommuner i Telemark. Telemark University College
- Hobbs NT (1996) Modification of ecosystems by ungulates. *J Wildl Manage* 60:695-713
- Hofgaard A (2001) Inter-relationships between treeline position, species diversity, land use and climate change in the central Scandes Mountains of Norway. *Global Ecol Biogeogr* 6:419-429
- Horne P, Petajisto L (2003) Preferences for alternative moose management regimes among finnish landowners: A choice experiment approach. *Economics* 79:472-482
- Huffaker RM, Bhat R, Lenhart S (1992) Optimal trapping strategies for diffusing nuisance-beaver populations. *Natural Resource Modelling* 6:71-97
- Johansson P-O, Kriström B, Mattsson L (1988) How is the willingness to pay for moose hunting affected by the stock of moose? An empirical study of moose-hunters in the county of Västerbotten. *J Environ Manage* 26:171
- Kennedy J (1986) *Dynamic Programming: Applications to agriculture and natural resources*. Elsevier, London
- Kvamme M (1988) Pollen analytical studies of mountain summer farming in Western Norway. In: Birks HH, Birks HJB, Kaland PE, Moe D (eds) *The Cultural landscape, past, present and future* Cambridge University Press, Cambridge, pp 349-367
- Langvatn R, Loison A (1999) Consequences of harvesting on age structure, sex ratio and population dynamics of red deer *Cervus elaphus* in central Norway. *Wildl Biol* 5:213-223
- Langvatn R, Mysterud A, Stenseth NC, Yoccoz NG (2004) Timing and synchrony of ovulation in red deer constrained by short northern summers. *Am Nat* 163:763-772
- Lima SL, Zollner PA (1996) Towards a behavioral ecology of ecological landscapes. *Trends Ecol Evol* 11:131-135
- Loison A, Langvatn R (1998) Short- and long-term effects of winter and spring weather on growth and survival of red deer in Norway. *Oecologia* 116:489-500
- Loison A, Langvatn R, Solberg EJ (1999) Body mass and winter mortality in red deer calves: Disentangling sex and climate effects. *Ecography* 22:20-30
- Manly BFJ (2002) *Resource selection by animals : statistical design and analysis for field studies*. Kluwer Academic Publishers, Boston, USA

ES 419290: Production of red deer in Norway

- Manly BFJ, McDonald LL, Thomas DL (1993) Resource selection by animals: statistical design and analysis for field studies. Chapman & Hall
- Mattsson L (1990a) Hunting in Sweden: Extent, Economic Values and Structural Problems. *Scandinavian Journal of Forest Research* 5:563-573
- Mattsson L (1990b) Moose management and the economic value of hunting: Towards bioeconomic analysis. *Scandinavian Journal of Forest Research* 5:575-581
- Mattsson, L (1994) Att kvantifisera viltets jaktvärde. Umeå Arbetsrapport nr. 192
- McCullagh P, Nelder JA (1989) Generalized linear models. Chapman and Hall, London
- Meisingset EL, Krogstad Aa (2000) Hjortebeiting på eng: skader, registrering og metodikk. Oppsummering av beiteskadeprosjektet 1996-1999. Ressurscenteret i Tingvoll, Tingvoll
- Meisingset, EL, Veiberg, V, Langvatn, R (1997) Beiteskader på graseng av hjort. Ressurscenteret i Tingvoll
- Melis C, Buset A, Aarrestad PA, Hanssen O, Meisingset EL, Andersen R, Moxnes A, Roskaft E (2006) Impact of red deer *Cervus elaphus* grazing on bilberry *Vaccinium myrtillus* and composition of ground beetle (Coleoptera, Carabidae) assemblage. *Biodiversity and Conservation* 15:2049-2059
- Milner JM, Alexander J, Griffin C (2002) A highland deer herd and its habitat. Red Lion House, Letterewe estate
- Milner-Gulland EJ, Coulson T, Clutton-Brock TH (2004) Sex differences and data quality as determinants of income from hunting red deer *Cervus elaphus*. *Wildlife Biology* 10:187-201
- Moe D, Indrelid S, Fasteland A (1988) The Halne area, Hardangervidda. Use of a high mountain area during 5000 years - an interdisciplinary case study. In: Birks HH, Birks HJB, Kaland PE, Moe D (eds) *The Cultural landscape, past, present and future* Cambridge University Press, Cambridge, pp 429-444
- Mysterud A (1999) Seasonal migration pattern and home range of roe deer (*Capreolus capreolus*) in an altitudinal gradient in southern Norway. *J Zool* 247:479-486
- Mysterud A (2004) Temporal variation in the number of car-killed red deer *Cervus elaphus* in Norway. *Wildl Biol* 10:203-211
- Mysterud A (2006) The concept of overgrazing and its role in management of large herbivores. *Wildl Biol* 12:129-141
- Mysterud A, Austrheim G (2005) Ecological effects of sheep grazing in alpine habitats. Shortterm effects. *Utmarksnæring i Norge* 1-05:1-91
- Mysterud A, Langvatn R, Yoccoz NG, Stenseth NC (2001a) Plant phenology, migration and geographic variation in body weight of a large herbivore: the effect of a variable topography. *J Anim Ecol* 70:915-923
- Mysterud A, Langvatn R, Yoccoz NG, Stenseth NC (2002) Large-scale habitat variability, delayed density effects and red deer populations in Norway. *J Anim Ecol* 71:569-580
- Mysterud A, Stenseth NC, Yoccoz NG, Langvatn R, Steinheim G (2001b) Nonlinear effects of large-scale climatic variability on wild and domestic herbivores. *Nature* 410:1096-1099
- Mysterud A, Yoccoz NG, Stenseth NC, Langvatn R (2001c) The effects of age, sex and density on body weight of Norwegian red deer: evidence of density-dependent senescence. *Proc R Soc Lond Ser B* 268:911-919
- Nilsen EB, Skonhoft A, Mysterud A, Milner JM, Solberg EJ, Andreassen HP, Stenseth NC (2007) The role of ecological and economic factors in the management of a spatially structured moose population. *Wildl Biol* submitted ms.
- Noy-Meir I (1975) Stability of grazing systems: an application of predator-prey graphs. *J Ecol* 63:459-481
- Pettorelli N, Mysterud A, Yoccoz NG, Langvatn R, Stenseth NC (2005) Importance of climatological downscaling and plant phenology for red deer in heterogeneous landscapes. *Proc R Soc Lond Ser B* 272:2357-2364
- Pinheiro JC, Bates DM (2000) *Mixed-Effects Models in S and S-plus*. Springer, New York
- Punsvik T (2002) Når hjorteviltet truer biologisk mangfold. *Hjorteviltet* 12:22-23
- R Development Core Team . 2006. R: A language and environment for statistical computing. [2.2.0.]. Vienna, Austria, R Foundation for Statistical Computing.
- Senft RL, Coughenour MB, Bailey DW, Rittenhouse LR, Sala OE, Swift DM (1987) Large herbivore foraging and ecological hierarchies. *BioScience* 37:789-799
- Skonhoft A (1999) On the optimal exploitation of terrestrial animal species. *Environment and Resource Economics* 13:45-67
- Skonhoft A (2005) The costs and benefits of a migratory species under different management schemes. *J Environ Manage* 76:167-175
- Skonhoft A, Olaussen JO (2005) Managing a migratory species that is both a value and a pest. *Land Economics* 81:34-50
- Skonhoft A, Yoccoz NG, Stenseth NC, Gaillard J-M, Loison A (2002) Management of chamois (*Rupicapra rupicapra*) moving between a protected core area and a hunting area. *Ecol Appl* 12:1199-1211
- Sødal, DP (1988) Økonomisk verdsetting av elgjakt. Ph.d. Norwegian University of Life Sciences (UMB)
- Solberg EJ, Rolandsen CM, Heim M, Grøtan V, Garel M, Sæther B-E, Nilsen EB, Austrheim G, Herfindal I (2006) Elgen i Norge sett med jegerøyne. NINA rapport 125:1-197
- Statistics Norway (2006) Official hunting statistics of Norway. Statistics Norway, Oslo and Kongsvinger
- Storaas T, Gundersen H, Henriksen H, Andreassen HP (2001) The economic value of moose in Norway. *Alces* 37:97-107
- Swallow S (1990) Depletion of the environmental basis for renewable resources. *Journal of Environmental Economics and Management* 19:281-296

ES 419290: Production of red deer in Norway

- Swanson T (1994) The economics of extinction revised. *Oxford Economic Papers* 46:800-822
- Sylvén S (1995) Moose harvest strategy to maximize yield value for multiple goal management - a simulation study. *Agricultural Systems* 49:298
- Thomas DL, Taylor EJ (1990) Study design and tests for comparing resource use and availability. *J Wildl Manage* 54:322-330
- Veiberg, V (2000) Hjorteskader på granskog i Stryn - Bruk av Sogn og Fjordane Skogeigarlag sine takstdata frå 1997-1998., pp 1-19
- Veiberg V, Pettersen J (2000) Registrering og taksering av borkgnag på gran. Hjorteskadeprojektet. Rapport 3:1-32
- Veiberg V, Solheim H (2000) Råte etter hjortegnag på gran i Sunnfjord. Rapport fra skogforskningen 18/00:1-16
- Vospernik S (2006) Probability of bark stripping damage by red deer (*Cervus elaphus*) in Austria. *Silva Fennica* 40:589-601
- Woods SN (2006) *Generalized additive models: an introduction with R*. Taylor & Francis, CRC Press, London
- Worton BJ (1989) Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70:164-168
- Zivin J, Hueth BM, Zilberman D (2000) Managing a multi-use resource: The case of feral pig management in California rangeland. *Journal of Environmental Economics and Management* 39:189-204