Space use of red deer and its implications for management

Erling L. Meisingset

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Centre for Ecological and Evolutionary Synthesis
Department of Biosciences
Faculty of Mathematics and Natural Sciences
University of Oslo

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Preface

As I grew up on a small farm next to a deeryard, red deer and deer hunting have been a part of my life for as long as I can remember and probably determined my interests and choice of profession. I experienced my first red deer hunt as a 4-year-old boy sitting next to my father; I was excited and probably a bit terrified. At age 15, I shot my first deer, and at age 21, I met Rolf Langvatn. These milestones have affected me ever since!

There are many people who I wish to thank. I owe a great debt of gratitude to my three supervisors: Atle Mysterud, Leif Egil Loe and Atle Wibe. I met my primary supervisor, Atle Mysterud, approximately 15 years ago, and we immediately found a "tone" that developed into a unique collaboration and friendship. Atle, you are the "engine" of the red deer group, and with your deep understanding of ecology and genuine interest in ungulate ecology, you are an inspiration to me. Thank you for teaching me the craft of writing scientific papers, even though I will never match your skills. It has been a privilege to have a supervisor willing to return a much improved draft within hours. Thank you for the excellent collaboration so far; I hope we can continue to develop it in the future, in terms of both science and hunting!

Leif Egil, we met on Svalbard as early as 1996; you as an incoming student with Rolf Langvatn and I as a former. Although we were a good reindeer-catching team, we were joined by the red deer. Since our early work on "teeth" together, we have moved on to GPS data and space use. Without your knowledge of R and your excellent analytical skills, the analyses of the GPS data and this thesis would have been impossible. Our cooperation has been excellent, and as with Atle, I hope it will continue. To both you and Atle, thank you for your generous hospitality during my occasional drop-ins in Oslo.

Special thanks go to Rolf Langvatn. Rolf, I am very grateful that you welcomed me as a young student and brought me into the world of science in the early 1990s. Your fabulous skills concerning both red deer and the collection and care of scientific data were a vital education to me. Without you, I never would have become a scientist or (perhaps) a red deer "specialist", but I'll never meet your standard! Additionally, thanks to the red deer group for the many years of excellent collaboration, especially Arve Aarhus, Inger Maren Rivrud, Unni Støbet Lande, Vebjørn Veiberg, Barbara Zimmermann and Richard Bischof. Thanks especially to Øystein Brekkum, my right hand for many years on the red deer marking projects, for cleaning up my messes and helping me keep all of the information and data together. Without your enormous patience during the long nights of marking deer together, much less data would have been available for this research! Thanks also for your friendship and for pleasantly sharing our office for many years! I am also very grateful to all of the people who have assisted with the red deer marking in the various Norwegian municipalities and who made the data available for this PhD project.

To all of my great colleagues at Tingvoll, thank you for providing an inspirational environment since 2003. To Atle Wibe, my head and supervisor at Tingvoll, thanks for your patience and your support throughout my PhD program, and thanks to my close friends Henrik Brøseth, Tore Gjul and Ole Erik Hørstad, the best hunting team ever!

Finally, this work would not have been possible without the help and support of my family. To my mother, Tora, who nurtured my fondness for nature, I am forever in debt to you! I also honour the memory of my father Lars, who taught me about the mysterious world of red deer hunting. My dearest Åse, you have encouraged and supported me every step of the way and have always been there for me. To Lina and Mali, thank you for teaching me that life is much more than work and made me think about non-deer-related things when needed! Most importantly, Åse, Lina and Mali, you have enriched my life!

Tingvoll, May 2015,

Erling L. Meisingset

Content

Paper I - VI

Abstract

In the northern hemisphere many wild ungulate populations have increased in recent decades, both in terms of density and range expansion. These ungulate species impact human land-use objectives, such as s agriculture and forestry, and the amount of damage often increases with higher population densities. One of the most severe consequences of these increases in population densities is higher numbers of traffic collisions, but wild ungulates provide important economic resources through the production of game meat and recreational hunting. Understanding factors that cause animal populations to increase, decrease or remain stable is fundamental management. However, less attention has been paid to how ungulate space use patterns may be critical for management. Such information is clearly needed for a range of management issues. Indeed, demarcating populations and finding appropriate scales for population management are often problematic. Additionally, the costs and benefits of ungulate population may not be evenly distributed, and space of use of deer may markedly affect for example risk of traffic collisions.

The main aim in my thesis is to identify basic behavioural mechanisms determining space use in red deer (*Cervus elaphus*) at different temporal and spatial scales, and what consequences these movements has for population management. By analysing different environmental factors in relation to migration patterns and habitat selection, this thesis contributes to the general understanding of animal movements at both small and large scales. Additionally, the aim is also to increase applied knowledge by relating red deer space use and movements to roads and management borders at two administrative levels, and to determine the extent to which space use may contribute to harvesting vulnerability. I analysed data from up to 114 male and 349 female red deer marked with GPS collars from 72 municipalities in 7 counties in Norway from 2002-2012, and hunting data from 11 municipalities.

I show that roads affected red deer space use, but avoidance occurred only at small scales and during daylight. The frequency of road crossings was high at night, with no effect of road size, and crossings more often occurred close to pastures and in forested habitats. There was both spatial and temporal (seasonal) variation in the risk of red deer vehicle collisions (DVC). The DVC risk was positively related to the speed limit of the road and was higher in the winter season, but decreased with increasing distance to pastures. The relative risk of DVC increased at a higher rate closer to pastures and in winter, with an increasing level of productive forest cover. Clearing road edges resulted in a 53% reduction in DVCs during the winter season. The proportion of migrants varied from 38% to 100% among populations. Migrants moved uphill to higher altitudes during spring migration, and autumn migration was delayed as population density increased. The proportion of migrants decreased at high population densities, whereas the proportion increased with topographic variation. Migrants experienced substantially higher access to springness, and gain in springness increased the proportion of migrants. However, most deer moved rapidly during migration thereby “jumping the green wave” rather than “surfing the green wave” therefore they did not fully exploit the potential of the green wave. Furthermore, a positive relationship was found between springness and body weight in males, but not in females. These results suggest that a combination of avoidance of competition in high-density winter ranges, social fencing during summer in addition to the forage maturation and predation risk avoidance hypotheses, is needed to explain the migration patterns of northern ungulates. The annual home ranges of both sexes, especially migrants, considerably exceeded the size of management units and questions the current spatial scales of management. In particular, migratory deer used a high number of municipalities and management units throughout the year, but most deer spent their time in one or two core management units. Crossing peaked during migration periods and was much higher in migratory than in stationary deer, and the frequency of border crossings was higher in males. The autumn migration period was spread throughout autumn and 80% of the individual migrations took place during the hunting season. The probability of being harvested on farmland decreased as the hunting season progressed, with a variable effect of age, but no effect of sex. Overall harvest numbers declined throughout the season, but the proportion of quota filled was positively associated with harvest numbers throughout the season.

The study revealed that small-scale space use is important to DVC risk; therefore, space use must be taken into account when planning mitigation measures along roads. Although reducing speed limit may be an unpopular mitigation effort, it is most likely effective at reducing DVC risk, especially in high-risk zones close to pastures. Therefore, speed limit reduction combined with clearance of vegetation along road edges will be a cost-effective tool for reducing DVC risk. The analyses of our extensive dataset across a considerable geographical range showed that landscape level patterns are important for the propensity to migrate, migration distance and home range size in red deer. Although roads do not seem to hamper daily or migratory movements, landscape characteristics are important when considering migratory movements at larger scales. For populations managed by hunting, the seasonal range expansion in spring and range contraction in autumn, are important for understanding for future distribution of deer. My thesis provides novel insights into the behavioural mechanisms underlying space use at different spatial and temporal scales, and this knowledge may benefit

the management of many species and ecosystems. I have further demonstrated that red deer use areas that are larger than the extent of the management units, thus identifying a mismatch between the spatial scale of management and animal space use that presents several challenges. The allocation of quotas and the definition of hunting periods need to account for migration patterns to optimise the harvest yield. However, knowledge of shared populations across current administrative boundaries is only the first step in developing unified management regimes. The main challenge is to find a consensus strategy for the different management units, which diverge in terms of the damage inflicted by deer, benefits received from hunting, and the harvesting regime. The next step will be to develop spatial models that can identify areas that likely to share a population.

List of papers

This PhD thesis is based on 6 individual papers. They are later referred to by their following Roman numerals:

I. Meisingset, E.L., Loe, L.E., Brekkum, Ø., Van Moorter, B., and Mysterud, A. 2013. Red deer habitat selection and movements in relation to roads. Journal of Wildlife Management 77: 181-191.

II. Meisingset, E.L., Loe, L.E., Brekkum, Ø., and Mysterud, A. 2014. Targeting mitigation efforts: the role of speed limit and road edge clearance for deer-vehicle collisions. Journal of Wildlife Management 78: 679-688.

III. Mysterud, A., Loe, L.E., Zimmermann, B., Bischof, R., Veiberg, V., and Meisingset, E. 2011. Partial migration in expanding red deer populations at northern latitudes - a role for density dependence? Oikos 120: 1817-1825.

IV. Bischof, R., Loe, L.E., Meisingset, E., Zimmermann, B., Van Moorter, B., and Mysterud, A. 2012. A migratory northern ungulate in the pursuit of spring: jumping or surfing the green wave? American Naturalist 180: 407-424.

V. Meisingset, E.L., Loe, L.E., Brekkum, Ø., Bischof, R., Rivrud, I.M., Støbet Lande, U., Zimmermann, B., Veiberg, V. and Mysterud, A. Spatial mismatch between management and movement ecology of a partially migratory ungulate. Manuscript.

VI. Rivrud, I.M., Meisingset, E.L., Loe, L.E., and Mysterud, A. 2014. Interaction effects between weather and space use on harvesting effort and –patterns in red deer. Ecology and Evolution 4 (24): 4786-4797.

Introduction

Many ungulate populations in the northern hemisphere have increased in recent decades both in terms of density and range occupation (McShea & Underwood 1997; Putman, Apollonio & Andersen 2011). The majority of these ungulate species are now widespread and with high population densities in many areas (Apollonio, Andersen & Putman 2010). In Scandinavia, cervid populations have increased remarkably over the last four decades with a multiplied harvest yield for landowners and hunters. However, the current high population densities may severely impact ecosystems at different levels (Mysterud 2006). They may change the composition and relative abundance of vegetation affecting both species composition and diversity (Cote et al. 2004), and alter other animal communities such as insects, birds and small mammals (Hegland, Rydgren & Seldal 2005; Melis et al. 2006; Foster, Barton & Lindenmayer 2014). The impacts of wild ungulate species can often conflict with human land-use objectives (McShea & Underwood 1997) such as agriculture and forestry and the degree of conflict and damage often are increases with increasing population densities (Gill 1992; Partl et al. 2002; Ball & Dahlgren 2002). One of the most severe consequences of these increases in densities is the increasing number of traffic collisions. With the expansion of road infrastructure and the rapid growth in traffic volume and vehicle speed, along with spread and the increase in the population densities of many ungulates, the number of road accidents involving wildlife has significantly increased (Apollonio, Andersen & Putman 2010; Langbein, Putman & Pokorny 2011). In 1993, the number of vehicle-ungulate collisions in Europe was estimated to 500 000 (Groot Bruinderink & Hazebroek 1996), but by 2005, the number ungulates annually killed in Europe was likely closer to 1 million (Langbein, Putman & Pokorny 2011). Since the early 1990s there has been a 3-fold increase in deer-vehicle collisions (DVC) in the US, totalling approximately 1.5 million in 2004 (Romin & Bissonette 1996; Langbein, Putman & Pokorny 2011). Thus, a major management goal is to find ways to mitigate these severe consequences. At the same time, ungulate populations provide important economic resources through the production of game meat and in recreational hunting, which is a significant source of revenue in many rural areas (Gordon, Hester & Festa-Bianchet 2004; Apollonio, Andersen & Putman 2010).

Information about the factors that cause animal populations to increase, decrease or remain stable is fundamental and vital for management (Gordon, Hester & Festa-Bianchet 2004). Long-term studies of ungulate population dynamics have provided an understanding of what factors that determine population size and composition (e.g., Clutton-Brock, Guinness &

Albon 1982), and many studies have focused on the effects of harvesting on population dynamics under different conditions (e.g., Langvatn & Loison 1999; Solberg et al. 1999; Nilsen et al. 2005). Other studies have modelled how to optimise the yield from exploited populations under different assumptions (e.g., Sæther, Engen & Solberg 2001). In contrast, much less attention has been paid to how ungulate distribution patterns may be critical for management. Such insight is clearly needed for a range of management issues. Indeed, demarcating populations and identifying appropriate scales for population management are often problematic; the costs and benefits of ungulates may not be evenly distributed, and space of use of ungulates may markedly affect for example the risk of traffic collisions. In this thesis, I focus on understanding how deer space use can be a critical component of deer population management.

An organism's movement and space use are driven by processes that act across multiple spatial and temporal scales (Morris 1987; Nathan et al. 2008). Space use may be simply defined as the locations used by an animal, independent of spatial scale (Kernohan, Gitzen & Millspaugh 2001) and habitat selection is defined as habitat use relative to the availability of all habitat types (Johnson 1980), where availability commonly refers to habitat selected at the spatial scales either within the study area or within the home range. Migration can therefore be seen as space use and habitat selection over large scales, and is particularly important for demarcation of populations and distribution of harvest offtake. Seasonal migration is defined as repeated, large-scale movements between distinct ranges (Bolger et al. 2008) and in seasonal environments, animals typically migrate between discrete summer and winter ranges, a strategy has evolved in response to the dynamic patterns of limiting resources (Avgar, Street & Fryxell 2013; Dingle 2014). Migrants are expected to achieve a selective advantage, either through enhanced access food supply or increased forage quality (Morgantini & Hudson 1989; Albon & Langvatn 1992; Hebblewhite, Merrill & McDermid 2008), decreased predation risk (Fryxell & Sinclair 1988), favourable weather patterns (Stenseth et al. 2002) and/or less competition over resources (Nelson 1995). While many studies have provided insight into the ecological drivers of migration (e.g., Fryxell & Sinclair 1988; Avgar, Street & Fryxell 2013; Dingle 2014), the implications for management and conservation have been considerably less well studied. Although the populations of many northern migratory ungulates are currently increasing, the long-term global trend is towards a reduction in migratory behaviour primarily due to anthropogenic habitat fragmentation and land-use change (Berger 2004; Harris et al. 2009). Reduced migration will lower the total carrying capacity of the environment, which would result in a population decline. Understanding the processes that underlie migratory behaviour, including the effect of anthropogenic barriers such as roads, is important for the conservation and management of migratory species (Milner-Gulland, Fryxell & Sinclair 2011).

Due to the extensive movements of many animals, there is often a mismatch between the spatial scale of the management units (e.g., protected areas, hunting areas or land under different landownership), and the spatial scales over which population processes operate (Lovell, Mandondo & Moriarty 2002). In terrestrial ecosystems, few studies have incorporated the spatial aspects of large animal behaviour when designing management plans although several studies have demonstrated this need (Milner-Gulland, Coulson & Clutton-Brock 2000; Singh & Milner-Gulland 2011; Skonhoft et al. 2002). In most European countries, the landowners hold the hunting rights and own the the outcome from the harvest (Apollonio, Andersen & Putman 2010), but interdependency between the different landowners will often exist. In the highlands of Scotland, for example, optimal management of the red deer at the level of the individual landowner was dependent on the management strategies on neighbouring estates due to sex- and density-dependent dispersal (Clutton-Brock et al. 2002). Further, under a unified management regime, neglecting migration may have led to sub-optimal population sizes of migrating moose (*Alces alces*) and an overall economic loss, because there often is an asymmetry between the areas that benefit from harvesting and the areas that experience high browsing damage (Skonhoft 2005). Identifying factors that determine animal space use, i.e., migration patterns and large-scale habitat selection, is especially valuable when managing highly exploited animal populations living in heterogeneous landscapes. The study of partially migrating populations is considered to be the key to understand the mechanisms driving migration, because a variable proportion of the population migrates while the remainder is stationary year round (Chapman et al. 2011). This is a common feature of many populations of more solitary species in forested areas at higher latitudes (e.g., White et al. 2007; Bunnefeld et al. 2011a), and provide important study systems because variation in migration patterns across individuals and populations is a result of interactions between environmental conditions and the animals (e.g., Singh et al. 2012). Such populations may be difficult to manage because their distributions vary considerably both spatially (geographically) and temporally (across seasons). Thus, understanding the extent to which individuals in populations migrate, the distances they cover and the ranges they utilise is particularly important for population management and ecosystem conservation.

At the within-home-range scale, habitat selection and small-scale space use by animals are usually linked to daily foraging and resting rhythms (Morris 1992; Godvik et al. 2009). Such movements can also have important management implications. For example, daily small-scale movements by animals can cause traffic accidents when animals cross roads as part of their daily foraging routine. It is possible that roads are the type of human infrastructure with the greatest influence on space use of a wide range of organisms (Forman & Alexander 1998; Trombulak & Frissell 2000; Fahrig & Rytwinski 2009), including ungulates (Gagnon, Schweinsburg & Dodd 2007). Roads may act as barriers to more large-scale animal movements and seasonal migrations, as they result in fragmentation and habitat loss (Spellerberg 1998; Vistnes et al. 2004) and they may also act as semipermeable structures, inhibiting animal movement and space use behaviour to a certain extent, and increasing mortality risk (Frair et al. 2008). Landscape and habitat features play an important role in determining where animals cross roads, and DVC risk zones are often associated with a number of factors (Seiler 2005; Langbein, Putman & Pokorny 2011; Gunson, Mountrakis & Quackenbush 2011) including road density (e.g., Frair et al. 2008), road type and vehicle speed (e.g., Danks & Porter 2010; Neumann et al. 2012), traffic volume (e.g., Bashore, Tzilkowski & Bellis 1985), roadside habitat characteristics (e.g., Malo, Suarez & Dìez 2004), habitat patterns in the wider landscape (e.g., Danks & Porter 2010; Neumann et al. 2012), time of day (e.g., Haikonen & Summala 2001) and season (e.g., Neumann et al. 2012). Analyses of habitat selection by animals in relation to road infrastructure at smaller scales and the temporal and spatial patterns of DVC risk may yield important information that can be used to target mitigation measures and how to manage high-density cervid populations in a highly human dominated landscape.

The main aim of my thesis is to identify basic behavioural mechanisms that determine space use in red deer at different temporal and spatial scales, and the consequences of these movements for population management. By analysing different environmental factors in relation to migration patterns and habitat selection, this research contributes to the general understanding of animal movements at both small and large scales. A further goal is to increase the applied knowledge by relating space use and movements to roads and management borders at two administrative levels, and to what extent space use may contribute to harvesting vulnerability. The Norwegian red deer population is a highly suitable study system, as individuals frequently switch between foraging in open agricultural pastures and hiding in closed forested habitats (Godvik et al. 2009). In addition, red deer are partial migrants were migrating individuals move to summer ranges to achieve higher food quality for a prolonged time (Albon & Langvatn 1992; Pettorelli et al. 2005a), and the population is managed through a selective harvesting regime (Milner et al. 2006).

I have analysed detailed GPS movement data from up to 437 GPS-marked red deer from seven counties covering most of the species' distribution in Norway, as well as harvest data including the habitat of harvest, age, sex and cull date from 11 municipalities. More specifically, I aim to do the following for each paper:

Paper I. Determine habitat selection and movement in relation to roads by analysing avoidance and crossing behaviour using a habitat selection framework.
Paper II. Identify risk factors influencing red deer – vehicle collisions (DVC) and test the effect of clearing the vegetation along road edges in an effort to prevent DVC.
Paper III. Investigate environmental factors that determine the proportion of migrating red deer by testing four hypotheses for partial migration.
Paper IV. Investigate the spatiotemporal relationship between plant phenology and landscape-scale movement patterns based on the forage maturation- and the green-wave hypothesis.
Paper V. Quantify how well red deer space use matches the spatial scale of administrative management levels across populations differing largely in topography and other environmental factors.
Paper VI. Investigate how the proportion of the red deer harvested on farmland and total off-take are affected by hunter effort, weather and moon phase and how this vary with sex and age classes.

Study species

History of the population of Norwegian red deer

Red deer is one of the most widespread and studied deer species with indigenous populations mainly being found in the temperate zones of Eurasia and North-America (Clutton-Brock, Guinness & Albon 1982). The widespread distribution and large body size of red deer makes it an important game species (Milner et al. 2006) and the Norwegian population represents the northernmost distribution range of red deer in Europe (Apollonio, Andersen & Putman 2010). Genetic analyses support three different subgroups within Europe based on mitochondrial DNA: western European (Iberia), eastern European (Balkan) and Mediterranean red deer (Sardinia, Skog et al. 2009; Niedzialkowska et al. 2011; Ludt et al. 2004). These three lineages most likely represent three distinct refuges during the Last Ice Age, and red deer expanded on from the Iberian refuge into western and northern Europe and from the Balkan refuge into eastern Europe (Skog et al. 2009; Niedzialkowska et al. 2011) as the ice sheet retreated through several oscillations. The glacial reduction of the sea level had created land bridges that in northern Europe connected the continent with the British Isles and the southern part of the Scandinavian Peninsula (Andersen & Borns 1997).

Archaeological findings indicate that red deer colonized Sweden about 10600 years ago, and Norway about 8500 years old (Rosvold 2013). The prehistoric distribution may have been wide in Norway, although most of the prehistoric findings have been made along the west coast (Ahlen 1965; Rosvold 2013), in the areas with the highest current densities. The Norwegian red deer population had probably a wide distribution during the Middle Ages and onwards, indicated by records of considerable export of skin and antlers (Collett 1909; Grieg 1909). In more recent times, written records states an abundant population across southern Norway in the sixteenth century, but in the seventeenth century red deer had become a rare sight and the distribution seem to have been reduced (Ingebrigtsen 1924). During the eighteenth century, the population was severely reduced and in the late nineteenth century it was limited to a few distinct localities along the west coast, probably counting only a few hundred individuals (Ingebrigtsen 1924). The reason for the severe population decrease was probably a combination of large carnivore populations (especially wolves and bears) and few hunting regulations, together with high human exploitation of natural red deer habitats and competition with grazing domestic animals.

Based on five distinct areas along the west coast the red deer have spread to most of southern Norway during the past 100-120 years (Haanes et al. 2010). Particularly after 1970 has the geographical range expanded to large parts of the country north to the polar circle (Langvatn 1988; Langvatn 1998; Meisingset 2008; Figure 2). Red deer are today common in most parts of southern Norway, and annual harvest occur in 15 out of 19 counties. The red deer harvest increased more than 10-fold since 1970 with a mean yearly increase of 6 % (Figure 1; Statistics Norway 2015), reflecting a concurrent increase in population size similar to many other deer populations in Europe (Apollonio, Andersen & Putman 2010). The direct proximate cause for increased density and expansion is due to changes in hunting regulations, with introduction of the quota system for hunting (from 1951) and later regulated specific age and sex specific quotas (from 1970). This change in the management system lowered hunting pressure on adult females at the expense of calves and males. The sex biased hunting regime has led to skewed sex ratio towards females in the population and a high population growth rate due to under-harvesting in total numbers (Langvatn & Loison 1999), but it has slightly changed the last 15 years toward a less skewed sex ratio (Solberg et al. 2012). Likewise, population growth seems to have stopped and harvest number has levelled off (Figure 2). The total population in Norway today counts probably around 150 000 individuals after the hunting season, with highest densities along the west coast.

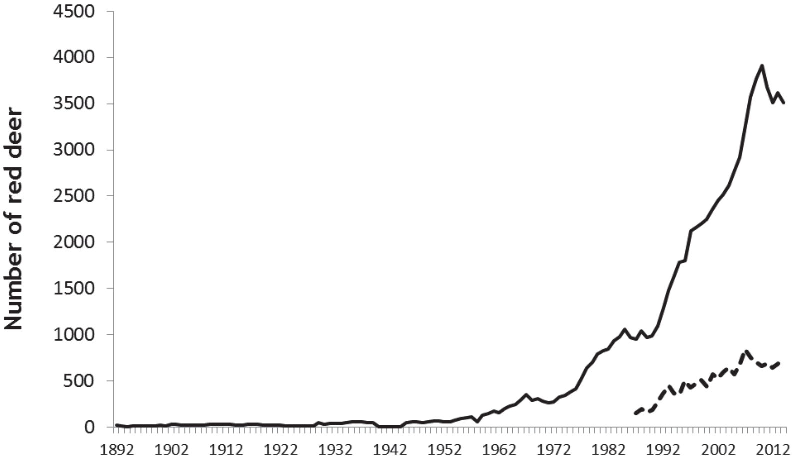

Figure 1. Number of harvested red deer (x 10) in Norway from 1892 to 2014 (solid line) and number of car killed red deer from 1987 to 2013 (broken line; Statistics Norway 2015b).

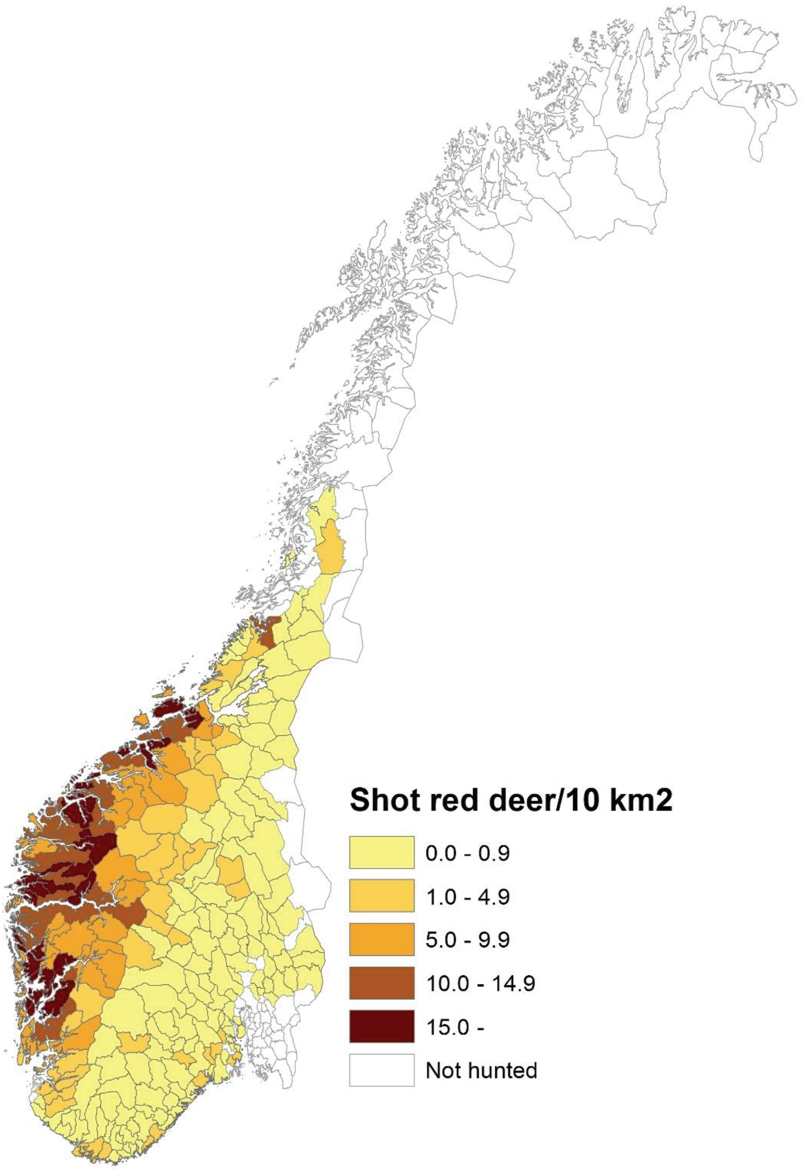

Figure 2. Distribution of red deer harvest in Norway based on harvest number per municipality in relation to counting area in 2014 (Statistics Norway 2015b).

Biology of red deer in Norway

The red deer is a sexually dimorphic species with large differences in body weight between sexes (Langvatn & Albon 1986; Mysterud et al. 2001b; Solberg et al. 2012). Body mass increases rapidly until 4-6 years old age (Langvatn & Albon 1986; Meisingset & Langvatn 2000) and typical maximal live weight are 180-240 kg in males (7-10 years old), while adult females weight usually range from 100 to 140 kg (5-13 years old). There are spatially variation in body weight across the population range, due to variation in habitat quality (Mysterud et al. 2001a) and population density (Mysterud et al. 2001b; Solberg et al. 2012). Age at onset of senescence in body weight is about 20 years in females (regardless of density) and 10-12 years for males depending on population density (earlier in high density areas; Mysterud et al. 2001b).

Red deer can potentially reach a quite high age, and the oldest reported male is 18 years and female is 26 years (Mysterud et al. 2001b). However, since hunting mortality is high very few will reach such ages (Langvatn & Loison 1999). Also, since large predators are scarce across the red deer range in Norway (Chapron et al. 2014), hunting mortality mainly determines survival with the exception of calves (Loison, Langvatn & Solberg 1999). Other significant causes of death are vehicle collisions (Mysterud 2004) and severe winter conditions (affecting primarily calf survival), which is highly variable among years (Langvatn & Loison 1999; Loison & Langvatn 1998; Loison, Langvatn & Solberg 1999; Langvatn & Meisingset 2001). Analyses show that more than 80 % of the adult red deer (≥1 year old) in the population were eventually shot during the autumn hunt (Langvatn & Loison 1999). Males (≥1.5 years old) had approximately 50% annual survival rate during the two last decades in the twentieth century, whereas the corresponding values in females was more than 80%. With the sex and age biased hunting practice during this period, only about 35% of the population consist of males (Langvatn & Loison 1999). However, over the past 10-15 years, there has been a focus among managers on increasing the age and proportion of males in the population, which has led to less sex-biased hunting quotas and an increasing proportion of males (Veiberg, Nilsen & Ueno 2010; Solberg et al. 2012).

Age of first reproduction in females is 2 or 3 years of age and is highly dependent of body weight (Langvatn et al. 2004). In prime-age females (3-13 years old) annual ovulation rates are close to 100 %, and ovulation occurs earlier in the autumn up to 13 years of age and are more synchronous with increasing population density (Langvatn et al. 2004). From 13-15 years of age, the proportion of females ovulating starts to decline rapidly (Langvatn et al. 2004). Males most frequently mature as yearlings, but do not invest heavily in the rut before reaching

3-4 years of age (Yoccoz et al. 2002). Red deer females give birth to only one calf per reproductive event and are typical capital breeders. Mating takes place in October (median ovulation date is 15th of October; Langvatn et al. 2004), which coincident peak roaring activities (Loe et al. 2005) and weight loss among males (Mysterud et al. 2008). With some variation in timing, calving occur in June after about 8 month of pregnancy (mean calving date 16th of June; Loe et al. 2005). Birth weight of calves is around 8 kg (Langvatn & Meisingset 2001) and body weight of calves in their first winter is dependent of their mothers weight and age, and cohort (Loison et al. 2004). Red deer females and their calves often form matrilineal groups or clans, while males are solitary or form bachelor groups (Clutton-Brock, Guinness & Albon 1982). However, the degree of sociality is highly dependent on time of year. Social segregation peaks during calving and aggregation peaks during rut (Bonenfant et al. 2004). Male harems during rut is typically smaller compared to Scotland (Clutton-Brock, Guinness & Albon 1982), but comparable to populations in France (Bonenfant et al. 2004).

Red deer are classified as mixed feeders (Hofmann 1985) with a variety of plant species in their diet. During summer, their preferred diet is herbs and grass (Albon & Langvatn 1992), whereas in winter shrubs (mainly bilberry [*Vaccinium myrtillus*]) and other types of browse are utilised (Mysterud 2000). However, a variety of grasses seems to be preferred during all seasons because during most of the year they prefer foraging at agricultural pastures at nighttime (Godvik et al. 2009), were in particular females select intensively fertilised meadows of intermediate age (Lande et al. 2014). Winter ranges is typically situated at lower elevations and/or close to the coast (Albon & Langvatn 1992), and often with greater access to farmland (Godvik et al. 2009), mostly due to increasing presence and depth of snow inland and at higher elevations during winter (Mysterud et al. 2001a). However, new inland habitats has been adopted over the last decades in line with the increasing population (Meisingset 2008). The red deer prefer forage- and cover rich habitats often with high productivity (Godvik et al. 2009). Summer habitats are often high-elevation forested areas in steeper slopes, whereas they avoid barren mountains (Loe et al. 2012).

The management and hunting of red deer in Norway

The Norwegian red deer management is organized hierarchically in 3 levels. Central authorities (Norwegian Environmental Agency) make general laws and regulations for the management and hunting (including regulation of the hunting period), whereas local authorities (municipalities) implements the regulations from central authorities. Landowners have exclusive hunting rights to ungulates and must create management units (MU) to access hunting quotas. About 80 % of the land area is privately owned in Norway (Statistics Norway 2015a). Typical property sizes for landowner which includes outlying field range from 0.3 to 1 km² in the various counties in the study, and less than 3% are >20 km² (Statistics Norway 2015a). This means that several landowners usually must join to create a MU. Municipalities should create a "counting area" stating the size of the quotas relative to a given area. This counting area should cover suitable habitats for red deer, usually most area under the tree line. In addition, the municipalities must create a "minimum required area", which is the smallest MU area that is needed to get a yearly quota of one deer. MU must apply for a hunting quota through a management plan that should be approved by the municipalities. The management plan should include goals for development of the red deer population within their area for the next 3 to 5 years, a plan for the number of deer hunted per year, and the desired quota divided by different sex and age categories (calves, yearling and older deer of each sex) per year in the period. Smaller MU (typically under 15 km²) can get a yearly quota by the municipality without a plan, and then only based on the minimum area of the municipality. MU's are often divided into hunting areas, where hunting teams organize the hunting in practice. The hunting season varied between municipalities and years during the study period. The hunting season started on September 10th in the study period 1999-2011, whereas from 2012 the onset of hunting was advanced to September 1st. During the first part of the study period (1999-2006), the hunting season was open until 15th of November, whereas in the last period (2007-2012) the hunting season was open until November 30th or 23th December. A rutting break in the hunting season from September 26th to October 10th was present in specific municipalities during certain years in the first part of the study period (see PAPER VI).

Large game hunting in Norway has traditionally been grounded in hunt for meat and recreation rather than for trophies (Milner et al. 2006). A variety of hunting methods is used in the hunting after red deer, with drive hunting without dogs as the most widespread. Although open agricultural land makes up only a small proportion of the landscape, stand hunting in these areas is common and about 50 % of all animals is shot there (Meisingset 2008). Other methods as call hunting males during the rutting season, still hunting and drive hunting with dogs comprises a small percentage of the total harvest. Hunters have access to all parts of the red deer's habitat included in their MU's area and hunting occurs around the clock, with distinct peaks during twilight hours at dusk and dawn especially at agricultural areas. Night hunting is undertaken during moonlight in open areas. All hunting is done with rifles.

Study area

The study area cover most of the red deer range in Norway, and was divided into seven different regions that represent different counties (Figure 3). These seven regions cover both the historical core coastal areas of southern Norway, and the recent areas east of the central mountains. The seven regions cover large differences in population density, and there are significant differences in topography and climate. Population density is highest in the coastal western regions and lowest in the eastern regions, and more than 95 % of the annual harvest in Norway occurs in the five core counties along the west coast. Total annual harvest in Norway was 35 135 red deer in 2014 (Statistics Norway 2015b). Number of car killed red deer has also increased substantially in Norway the last three decades (Figure 2, Solberg et al. 2009), and the main reason seems to be an effect of increasing deer population size and increasing traffic burden (Mysterud 2004). Within our study area there has been an increasing rate of car killed red deer the two last decades, with annually 140–160 red deer killed (Meisingset et al. 2010).

The topography along the west coast is characterized by large variations, with steep terrain, high mountains and fjords and is more heterogeneous than the northern and eastern regions. Mountain areas account for a substantial proportion of the area in the western regions, but the coast has a lower elevation gradient than further inland (in the fjords). The northern regions is characterized by large and long valleys, whereas the eastern regions have less topographic variation and is characterized by gently sloping hillsides and along valleys. The west coast has a typical oceanic climate and precipitation decreases generally from south to north along the west coast, and from the coast to inland, with fjord landscape in between. The summers are relatively cool, whereas winters usually are short and mild the latitude taken into account, especially by the coast. The eastern regions has a more continental climate, with colder and drier winters, and warmer summers. Snow depth and duration of snow cover vary significantly between coastal and inland areas, and with increasing altitude.

The west coast belongs to the boreonemoral zone, but the furthest south on the west coast there are elements of the nemoral zone (Moen 1998). The northern and eastern regions belong to the southern boreal zone. Treeline elevation increases with distance from the coast and is generally higher in north and east than in west. Along the west coast forests are characterized by native pine (*Pinus sylvestris*) and deciduous forests, but with substantial elements of Norway spruce (*Picea abies*) is planted in the most productive areas. In the north and eastern regions Norway spruce is dominating, but often in a mix of pine and deciduous trees. The most common deciduous tree species are rowan (*Sorbus aucuparia*) and birch (*Betula* *spp*.), but along the west coast there are also strains of more thermophilous deciduous forests (Speed et al. 2013). Juniper (*Juniperus communis*) and a mixture of young deciduous and coniferous trees often dominate forest undershrub. The most common species in the field layer are bilberry, but usually there are significant amount of other heathers, grasses and herbs (Speed et al. 2014).

Human land-use patterns have changed considerably in Norway in the last century. Both agriculture and forestry has undergone dramatic changes since the World War, with substantial effects on the vegetation. For example has rough livestock grazing decreased markedly on outfield pastures (Austrheim, Solberg & Mysterud 2011), while timber harvest and planting of trees has increased. This has probably made more areas suitable as red deer habitats. Agricultural areas are mostly located in lower and flatter parts of the landscape, but account only for a small part of the total area. Along the west coast and in north, is grass production (dominated by timothy [*Phleum pretense*], meadow fescue [*Festuca pratensis*] and meadow grass [*Poa* spp.]) for livestock (and grazing of livestock) the main output, while in east a significant amount of grain production occurs along with grass production. Towns, roads, and other human infrastructure are mainly located in the lower elevations of the landscape (PAPER I; PAPER II). Roads are distributed across the whole study area and in all habitat types, but at quite low densities in most areas (Table 1 in PAPER I).

Material and methods

Marking of red deer

Red deer were captured at feeding sites from January to early April each year in the period from 2002 to 2012, were they naturally had winter ranges. Darting was carried out during dark hours from a blind or motor vehicle at supplemental feeding stations often with artificial light. Deer were immobilized by dart injection of xylazine and tiletamine-zolazepam from a distance of 10-30 m, using a CO_2-powered gun and lightweight 2.0 or 3.0 ml darts (Sente et al. 2014). When animals were recumbent, they were approached slowly, blindfolded and kept lying down. Animals were monitored during immobilization and through recovery after drug reversal with atipamezole (Sente et al. 2014). All animals were marked with ear tags (Allflex Super Maxi Tag, 75-97 mm, Allflex, Denmark) and fitted with GPS collars suitable for red deer females and males, respectively (Tellus from Followit, Sweden, and GPS ProLite from Vectronic, Germany; collar weight: 750-850 g, 0.5-1.0% of animal body weight). For all marked red deer we recorded body weight, measured hind foot length, estimated age based on tooth development and/or tooth wear, and took samples for various purposes. Permits to capture and mark animals were granted by the Norwegian Animal Research Authority (NARA; ref no. s-2006/28799; permit no. FOTS ID 4863), and the Norwegian Environment Agency (ref no. 2006/5393). All field personnel marking red deer were approved by NARA.

Red deer data

I had access to GPS data from up to 114 male and 349 female red deer marked in 72 municipalities from 7 counties of Norway in the period 2002-2012 (Figure 3, Table 1). However, sample sizes varied in the various papers. In PAPER V most of the dataset was used, whereas subsets were used in PAPER I, PAPER II, PAPER III and PAPER IV. In PAPER I and PAPER II was GPS-data from region N and NW used, whereas in PAPER III, PAPER IV and PAPER V was data from all the regions used. Female collars provided one location every hour, whereas male collars generally provided positions every 2 hour. However, during the period from 1 September to 1 December male collars took positions every 20 min. Most of the collars provided locations from one to for up to 2 years and most collars supported wireless download of data over the GSM telecommunications network. Mean GPS fix rate was 90.2 % (range 45.2–100 %) and median location error has been estimated to 12 m (Godvik et al. 2009).

Table 1. Number of GPS marked red deer from 2002 to 2012 divided into sex and study region (N=Sør-Trøndelag, NW=Møre & Romsdal, W=Sogn & Fjordane, SW=Hordaland, S=Rogaland, SE=Buskerud, E=Hedmark).

Sex/Region	N	NW	W	SW	S	SE	E	Sum
Females	27	82	96	67	19	21	37	349
Males	25	39	14	35	0	1	0	114
All	52	121	110	102	19	22	37	463

Collision, harvest and environmental data

The number of car killed red deer within the study area in PAPER I and PAPER II was recorded to 306 during the two year study period, were 271 DVCs was found within the combined 100% minimum convex polygon home range of the GPS-marked red deer. The DVCs had location accuracy (recorded with handheld GPS; ±10 m) comparable with the accuracy of the red deer collar positions and was obtained from the municipalities or from Statistics of Norway (Statistics Norway 2015b). The experimental vegetation removal tested in PAPER II was conducted along a 32 km along Highway 70 in the valley of Sunndal during summer 2008 in cooperation with the regional road authorities. All vegetation up to 8 m from the road shoulder was removed to increase visibility along the road edges and emerging vegetation in this area was cut yearly to prevent substantial regrowth. DVC data along this highway section and a 35 km control stretch at Highway 65 in the neighboring valley Surnadal were collected in the period 2003–2010. In total was data collected from 207 DVC, 137 at Highway 70 (103 occurring before and 34 occurring after clearance) and 70 at Highway 65.

The harvest data and counting areas on the scale of municipalities was obtained directly from the municipalities or from Statistics of Norway (Statistics Norway 2015b). In PAPER V we had access to exact information about borders and harvest data of all MUs in 2 of 7 study populations (NW and N), which we obtained from the municipalities. The harvest data in PAPER VI was from harvested red deer in 11 municipalities in the study regions N, NW, W and SW and was obtained from the municipalities. Hunters provided data on harvest record and hunter effort during 1995 and 1999-2010 during the hunting season. These data derive from the "seen deer" data scheme that is mandatory by law in Norway when hunting cervids and data are regarded highly reliable (Solberg & Sæther 1999; Mysterud et al. 2007). Hunters noted the number of harvested deer and their sex and age class (calf, yearling or older), the number of

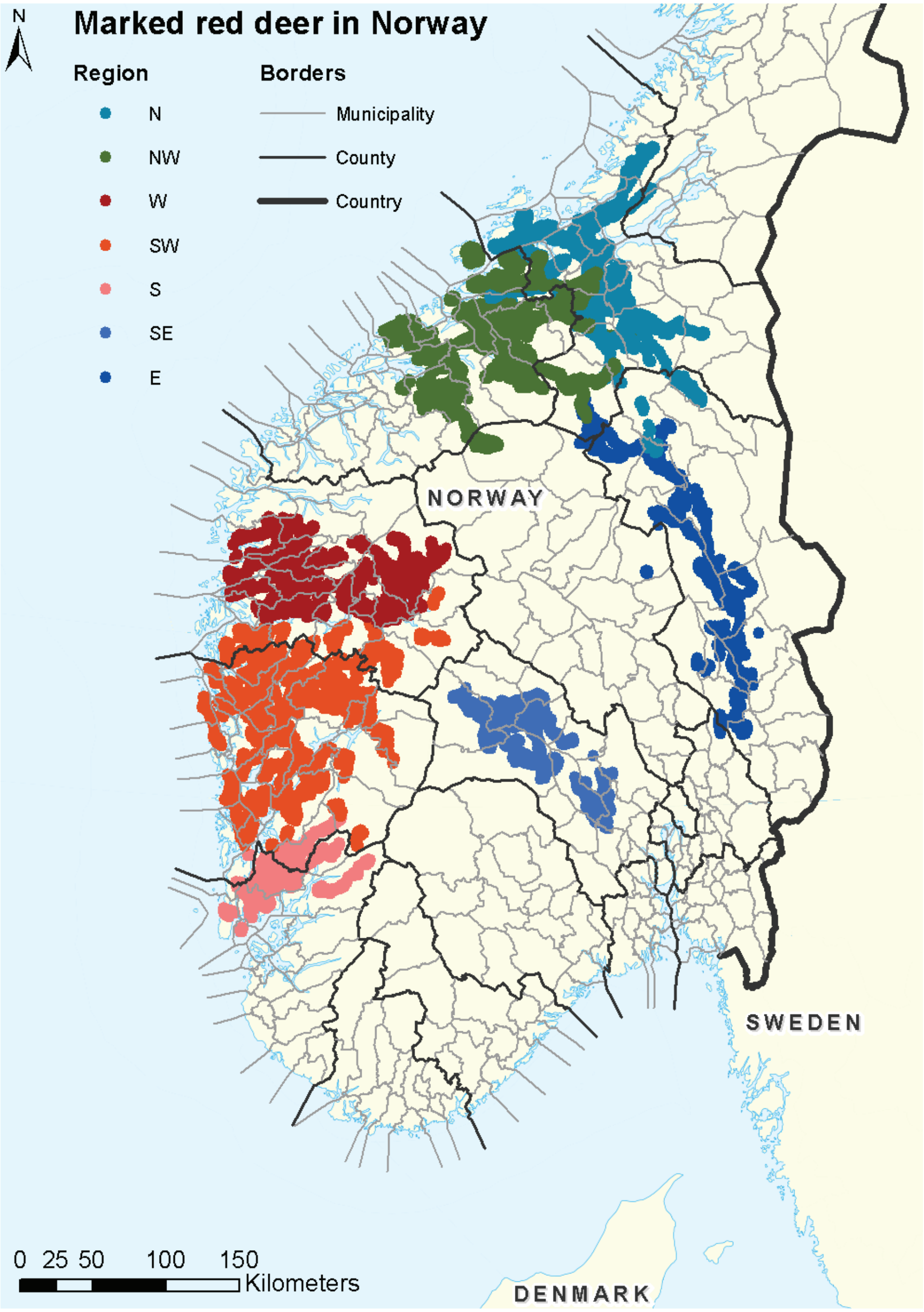

Figure 3. GPS locations divided into the 7 study region/counties in Norway. Colours represents the different study regions (N=Sør-Trøndelag, NW=Møre & Romsdal, W=Sogn & Fjordane, SW=Hordaland, S=Rogaland, SE=Buskerud, E=Hedmark) and dots are individual GPS positions.

hunters participating and hours spent hunting. They also noted if the individual was shot on farmland or in forested habitat. Data were available in time series of 2-12 years from the different municipalities, and included 19 764 harvested red deer.

Digital terrain models and land resource maps were provided by the Norwegian Forest and Landscape Institute (NIBIO 2015), while data on municipality borders were obtained from The Norwegian Mapping Authority (Kartverket 2015). We obtained road data and road classification from the Norwegian road authority (Vegvesen 2015). Weather data were recorded by meteorological stations located within the study area and downloaded from Norwegian Meteorological Institute (NMI 2015). Data on day light and the moon phase were downloaded from the United States Naval Observatory (United States Naval Observatory 2009).

Results and discussion

Habitat selection and roads (PAPER I)

Deer–vehicle collisions has increased substantially in many countries in parallel with increasing population densities with major social, economic and animal welfare costs (Groot Bruinderink & Hazebroek 1996; Langbein, Putman & Pokorny 2011; Mysterud 2004). A number of studies have documented avoidance of roads in ungulates (e.g. Dyer et al. 2001; Rowland et al. 2005; Frair et al. 2008; Laurian et al. 2008), and may act as barriers for animals movements, resulting in habitat loss (Spellerberg 1998; Vistnes et al. 2004) and redistribution of individuals (Wisdom, Cimon & Johnson 2005; Gagnon et al. 2007). However, roads are often in flatter terrain suitable for agriculture, which provide attractive forage for grazers such as various species of deer (e.g. Godvik et al. 2009). Roadside vegetation may also in itself be nutritionally beneficial (Finder, Roseberry & Woolf 1999), resulting in a food-driven attraction towards roads. Therefore, knowledge of animal behaviour in relation to road networks is necessary to assess the effect of road development on wildlife and to implement appropriate mitigation measures.

By using data from 67 GPS-marked red deer from Møre & Romsdal and Sør-Trøndelag counties (population NW &N, Figure 3), we quantified 1) scale of avoidance of roads, 2) crossing frequency, and 3) selection of crossing sites by GPS-marked red deer. We predicted that avoidance behaviour should increase with increasing road size (traffic burden), in open habitats and be higher at daytime than at nighttime. Further, we predicted that crossing frequency decreased with road size, and be higher at nighttime than daytime. We expected also higher frequency during migration phases (seasonal variation). Lastly, we predicted that crossing should occur more often in dense habitats, and close to pastures.

Our analyses showed that red deer crossed roads frequently (about 2 road crossings per day), and it did not depend on traffic burden (Figure 4). However, crossing frequency was strongly affected by season and light conditions, and females crossed more often than males in all seasons (Figure 4). Red deer crossings of roads occurred closer to pastures (Figure 5), in flatter terrain, and sites with greater proportion of productive forests cover than at random locations along roads. Avoidance patterns differed slightly from the road crossing results. We found that red deer avoided roads even at very low traffic burdens, but in contrast to road crossings, avoidance was more pronounced with increasing size of the road. However,

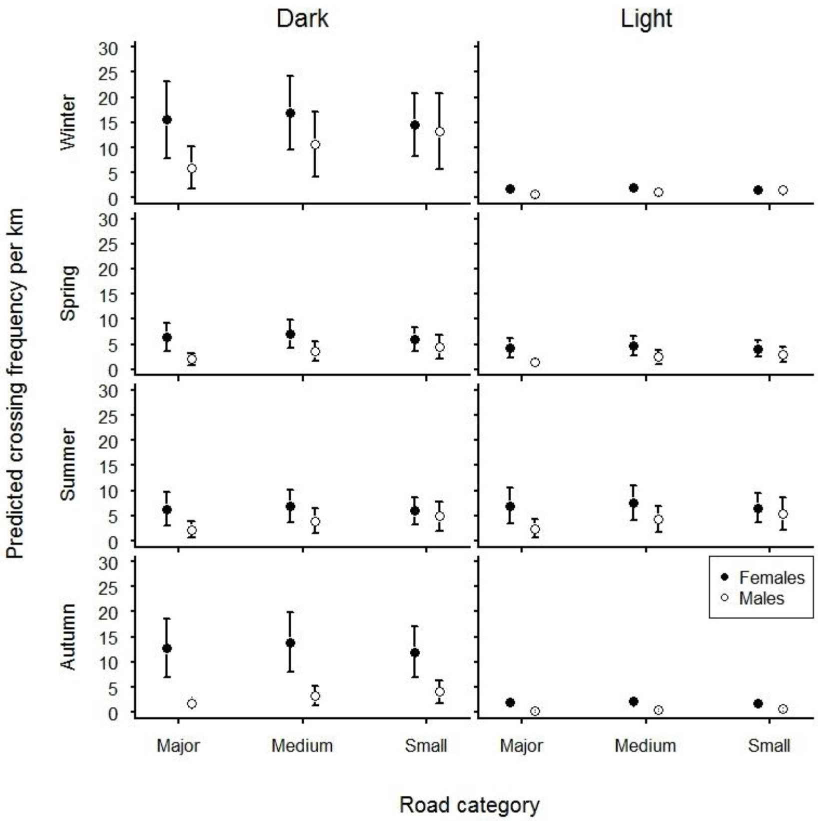

Figure 4. Predicted number of road crossings for female and male red deer per season and road category and separated for day and night conditions in Norway in 2007 and 2008. The estimated crossing frequencies are number of crossings per km of road stretch. Error bars are 95% confidence limits.

compared to the difference between day and night, was the effect of road size minor. Avoidance behaviour was found at very short distances from roads (50-100 m), whereas habitat conditions and season had no pronounced effect.

The spatial scale of avoidance varies across species and studies, which will markedly affect how important the ecological effect of roads are. Some studies show avoidance effects on quite long distances from the road (up to 500 m in moose; Laurian et al. 2008, up to 1800 m in elk; Rowland et al. 2000), but most studies show patterns of very local avoidance (e.g.

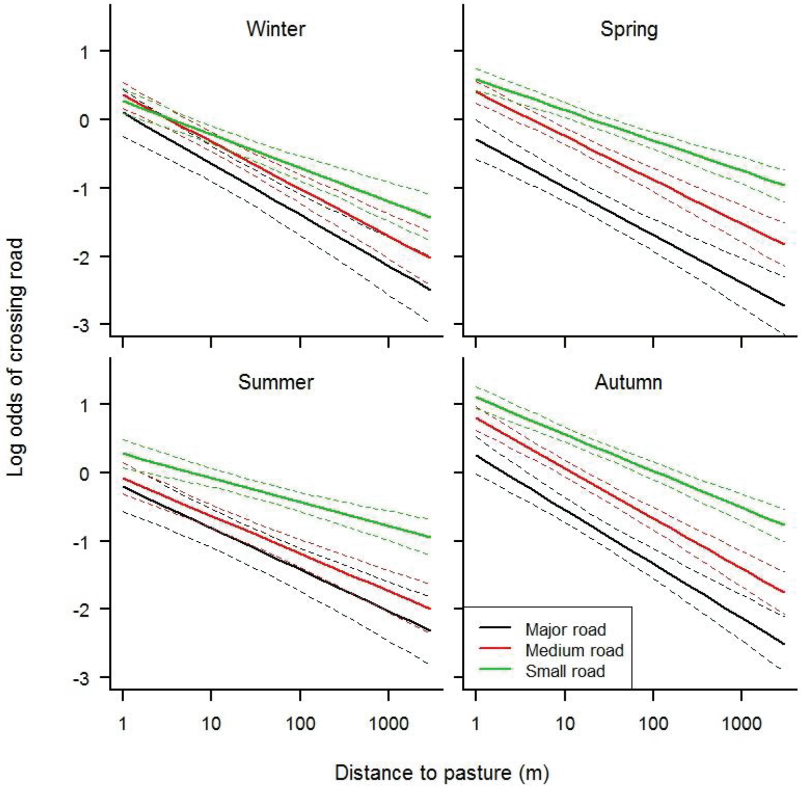

Figure 5. Log odds of red deer road crossing in relation to distance to pasture (in meters; log scale) for major, medium, and small roads during each season in Norway in 2007 and 2008.

Gagnon et al. 2007; Sawyer et al. 2007; St Clair & Forrest 2009). Habitat condition had minor effect on avoidance behaviour, in contrast other studies (e.g. Gagnon et al. 2007). However, in our study we analysed behaviour related to a single road, but multiple roads or cumulative road density can saturate a landscape and habitat loss can occur when road density exceed a certain threshold (Rowland et al. 2000; Frair et al. 2008). Although the deer avoided larger roads more than small roads, the decision to cross did not depend on traffic burden. Pastures are highly selected habitats during most of the year (Godvik et al. 2009) and road crossings is often motivated by directed movements to access pastures (Gagnon et al. 2007). The frequent road crossing by red deer in our study suggests that roads not were a major barrier for movement. My result suggests that the perceived risk of road crossing is small compared to the gain obtained by accessing pastures on the opposite side of even a major road or any other reason.

Greater crossing frequency at nights and during autumn and winter when traffic burden is less underlines that avoidance and crossing behaviour probably is related to vehicle traffic and human disturbance, similar to what is found in other studies (Gagnon et al. 2007; Laurian et al. 2008).

We also observed seasonal variation in crossing frequency with higher crossing rates during winter. The reason for this seasonal pattern is probably that red deer use lower elevation areas during this time of year (PAPER III), where both road and pasture density is greater (Table 1 in this paper). Roads are thus not likely strong barriers for seasonal migration between winter and summer ranges, even most migrating deer cross several roads of different categories during this movement phase. Migratory movements of red deer often happen during nights, further supporting that roads do not act as barriers for seasonal migration. In situations with weak avoidance behaviour and high road crossing frequency, together with low density of roads, it is likely that roads have low implications for carrying capacity and/or daily and seasonal movement behaviour in red deer. The high frequency of red deer road crossings, even at highways, suggests that mitigation measures may be effective if installed in the right areas. As crossings occur more often in dense forested habitats and close to pastures, make these areas in particular suitable and effective for mitigation measures.

Collision risk and mitigation for DVC (PAPER II)

More effective mitigation measures along roads are urgently needed in many areas (Langbein, Putman & Pokorny 2011). The number and variety of mitigation measures to reduce DVCs have thus increased greatly during recent decades (Iuell et al. 2003), but few mitigation measures have been evaluated scientifically (Langbein, Putman & Pokorny 2011). Predictive models of DVC sites are regarded as the key to mitigate accidents both at regional and local scales (Malo, Suarez & Dìez 2004; Gunson, Mountrakis & Quackenbush 2011) and are important for identifying relevant DVC risk factors. Modelling of accident risk relative to environmental characteristics could enable managers determine locations of mitigation measures or to plan the layout of new roads.

In this study, we developed two collision risk models by contrasting location data of DVCs with 1) random positions along roads, and 2) position data from GPS marked red deer within the study area in NW (Møre & Romsdal) and N (Sør-Trøndelag), in central Norway (Figure 1). We analysed position data providing road crossings from 67 GPS marked red deer and location data of 271 car-killed deer within the home ranges of the deer studied. We modelled collision risk as a function of speed limit, season, road characteristics, and habitat features. We further tested if vegetation clearance along a highway reduced the collision frequency of red deer.

Out of the available DVC sites, we found 83.0% on major roads, 17.0% on medium-sized roads, whereas we found none on small roads. The distribution of DVCs compared with random sites along roads differed considerably in relation to several of the predictor variables. The relative risk for DVCs increased with speed limit. A change in speed limit from 50 to 80 km/hr gave an increased DVC risk by 8.6 times. The increased in relative risk was dependent of traffic burden, i.e. lower for medium than for major sized roads, and increased with cover of productive forest and terrain ruggedness. Further, the DVC sites differed from red deer crossing sites for several of the variables. An increase in speed limit from 50 to 60–70 km/hr increased the relative risk by a factor of 6.8, whereas from 50 to 80 km/hr gave an increased risk of 14.4 (Figure 6). The relative risk for DVC was lower at medium-sized roads compared to major roads, and increasing speed limit had larger effect at major roads. The relative risk decreased considerably when distance to pasture exceeded 50 m and this difference occurred in all seasons (Figure 6). We found higher risk for DVCs during winter compared to the other seasons. With an increasing level of productive forest cover relative risk increased at a higher rate closer to pastures and in winter compared to other seasons. Road edge clearance in our study area gave a 53% reduction in DVCs during winter season (Figure 7). Interestingly, we found no effect of road edge clearance during summer.

In line with our results, have studies on collision sites of moose both in Sweden and western Maine, USA, previously reported higher probability of moose–vehicle collisions with increasing speed limit (Seiler 2005; Danks & Porter 2010; Neumann et al. 2012). The intuitive explanation is that increased speed gives the driver shorter time to respond when a deer crosses the road in front of the car and increased stop distance for the vehicle. However, our results also showed an interaction between road size and speed limit. Since the effect of speed limit was large on major than medium sized roads, other effects contribute also to the collision risk.

Light conditions vary substantially between seasons at northern latitudes, which probably are the main reason that we found highest risk of DVC during winter season. In the winter season, peaks in activity patterns are often found in the dark hours just after dawn and just before dusk (Godvik et al. 2009; Pepin, Morellet & Goulard 2009). This often corresponds with peaks in daily traffic level during the winter season. In northern summers, darkness is

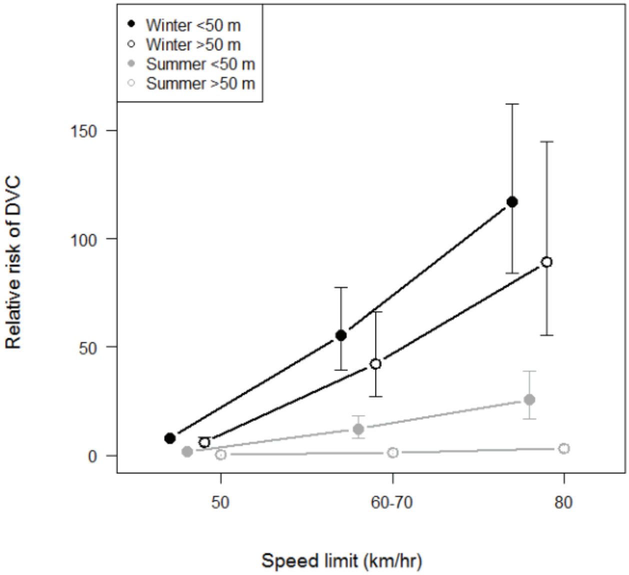

Figure 6. Relative risk (±SE) for red deer crossings ending in deer–vehicle collisions (DVC) as a function of speed limit (50, 60–70, and 80 km/hr) during summer (gray) and winter (black) seasons at 2 distance categories from pastures (<50 m: solid dots, >50 m: open dots). The predictions are based on the most parsimonious model. Predicted values are for major roads and for mean values of numeric covariates (productive forest cover = 20.9%).

virtually absent and therefore the proportion of meetings between cars and deer that occur during darkness is much higher during winter than other parts of year. In PAPER I we found that crossing sites is more frequent close to pastures and it is likely that red deer take higher risks when approaching pastures. Indeed, this correspond to our finding that DVC risk was higher close to pastures. Other studies have also highlighted that proximity to pasture seems to be an important factor when evaluating DVC risks (Tappe & Enderle 2007) and should be considered when planning mitigation measures (Gagnon et al. 2007). Target clearance along the roads has been increasing in recent years, in particular to reduce the number of collisions of moose and various deer species (Iuell et al. 2003). Our study showed that road edge clearance substantially reduced DVCs during winter season. Since we also found higher relative DVC risk with increasing cover of productive forest especially during winter in non-clearance areas, it is likely that the effect of road edge clearance at least partly a was car driver effect.

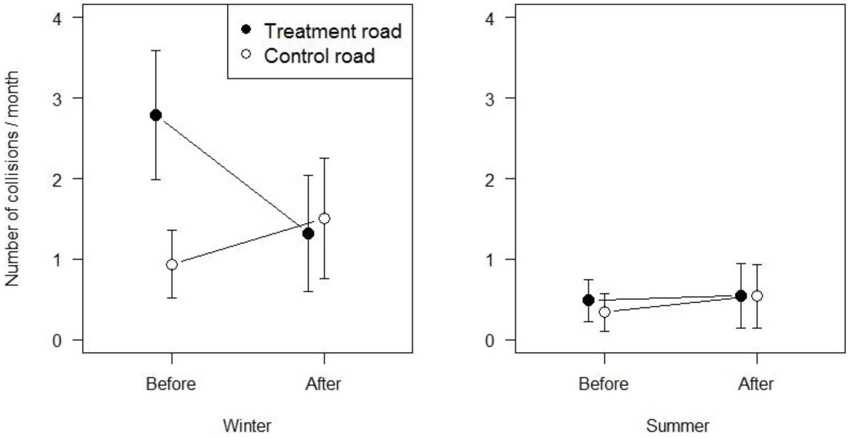

Figure 7. Predicted number of red deer–vehicle collisions (DVCs) per month (± 95% CI) at the treatment road (vegetation clearance; solid dots) and the control road (open dots), before and after roadside vegetation clearance and grouped into winter and summer seasons.

Thus, clearance gives better visibility along roadsides and possibilities for discovering deer earlier as they are approaching the road (Rea 2003). Corresponding figures for effect of clearing along roads are sparse for both moose and red deer in Scandinavia and elsewhere. However, several studies of ungulates show that risk of DVCs decreases with visibility near roads (Bashore, Tzilkowski & Bellis 1985; Nielsen, Anderson & Grund 2003; Malo, Suarez & Dìez 2004; Seiler 2005), but both local (small) and larger spatial scales of habitat characteristics are likely to be of importance (Seiler 2004). When assessing mitigation efforts it is therefore important to consider landscape characteristics at different scales. Temporal and spatial patterns in DVCs should be used to predict the optimal locations of deer crossing structures (sites with high risk of DVC; e.g., Clevenger & Waltho 2005), the seasonal timing of efforts, and how to manipulate habitat features or road characteristics to reduce collision risk.

Partial migration – a search for mechanisms (PAPER III)

Migration of large mammalian herbivores has been studied for centuries (Milner-Gulland, Fryxell & Sinclair 2011), with a considerable focus on explaining the benefits of migration (e.g. Albon & Langvatn 1992). However, the fact that not all individuals migrate in many populations has received less attention. Partial migration is for example reported for all native forest deer species in Scandinavia, both the small browsing roe deer (*Capreolus capreolus*; Mysterud 1999) and the large browsing moose (*Alces alces*; Histøl & Hjeljord 1993; Ball, Nordengren & Wallin 2001), as well as for the mixed feeding red deer (Albon & Langvatn 1992). Partial migration is particularly useful for studying the benefits of migration, as comparisons can be made to stationary animals. Though this investigated in quite a few single populations, few studies have quantified variation in partial migration across populations for a given species. It is well known that snow depth at high altitude forces migration to low elevation in fall (e.g. Mysterud 1999). A currently more interesting question is why migrants return to high elevation areas during summer.

The most commonly used hypothesis to explain migration is the forage maturation hypothesis (FMH; Fryxell and Sinclair 1988; Albon and Langvatn 1992; Hebblewhite et al. 2008). The main basis for this hypothesis is that at early phenological stages plants have higher quality as forage than the more matured stages. Migrating animals benefit therefore by following gradients in plant quality in the landscape. However, theoretical models of partial migration highlight a role of density dependence and competition (Kokko & Lundberg 2001) and that the understanding of migration cycles of large mammalian herbivores can be improved by considering it within a framework of seasonal population limitation (Bolger et al. 2008). Migration to high elevation summer ranges can serve as a strategy to avoid intraspecific competition due to high density in winter areas (Nelson 1995). Density may also affect conditions in potential summer ranges. In many large mammals there is a strong social organization especially during the breeding season (Comer et al. 2005; Miller et al. 2010), and it may be difficult to find summer ranges in a situation with high population density without social fences. The social fence hypothesis has mainly been addressed for explaining dispersal of small mammals and birds (Matthysen 2005). This hypothesis highlight that individuals are not free to use all areas due to presence of other animals.

In this study, we analyse data from 141 GPS-marked female red deer from our 7 regions in Norway (Figure 3). We aimed to test four hypotheses regarding partial migration in red deer to disentangle the likely mechanisms causing partial migration (for full list see Table 1 in

PAPER III): *The forage maturation hypothesis* (e.g. Fryxell & Sinclair 1988). We predict an increase in proportion of migrants in areas with access to large variation in altitudes (topographic diversity). *The competition avoidance hypothesis* (Nelson 1995; this study). We predict increased proportions of migrants with increasing population density at winter range. *The social fence hypothesis* (Matthysen 2005; this study). If there are social constraints or fences impeding establishment in high-density areas during the summer season, we predict a decreasing proportion of migrants as population density increases. *The predation risk avoidance hypothesis* (Barten, Bowyer & Jenkins 2001). If migration is to reduce predation on vulnerable offspring, we predict migration even at low density and no clear density dependent relationship.

The proportion of migrants varied from 38% to 100% among populations (Figure 8). We found a positive effect of topographic variation and a negative effect of population density on propensity to migrate in consistent with both the forage maturation (topography) and social fence hypotheses (density). Migrants moved uphill to higher altitudes during summer (Figure 8), whereas altitude of winter range was at a lower elevation at high population density. The last was contrary to the prediction of increased use of higher elevation at high density from the competition avoidance hypothesis. Migration distance decreased markedly with increasing population density. Autumn migration was later at high density, as predicted by the avoidance of competition hypothesis.

Migration is common at northern latitudes and at higher altitudes (e.g. Singh et al. 2012), and an obvious explanation is linked to strong spatial variation in seasonal limitations. The forage maturation hypothesis explains well uphill migration in spring (Fryxell & Sinclair 1988; Albon & Langvatn 1992; Hebblewhite, Merrill & McDermid 2008). It is therefore not surprising that topographic diversity, likely reflecting gradients in plant phenology and plant growth throughout the growing season (Pettorelli et al. 2005a), positively affected the probability of migration. However, we found also evidence for density dependence in proportion of migrants, but the pattern was opposite to the avoidance of competition hypothesis. The avoidance of competition hypothesis yields some novel predictions regarding details in the migration pattern, while the main altitudinal migration can fit all hypotheses (Table 1 in PAPER III). Our finding of delayed autumn migration with increasing density is supported by a study of white-tailed deer, where migrating deer spent minimal time in the winter areas, likely due to high competition in those areas (Nelson 1995). For roe deer, some migrants waited until snow depth forced them to the winter range (Mysterud 1999), whereas longer seasonal movements

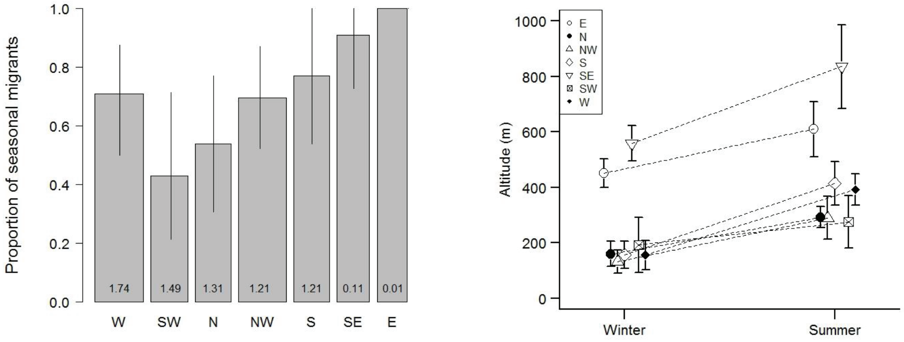

Figure 8. Barplot showing the proportion of seasonally migrating female red deer in each region of Norway only taking into account the individuals showing a clear migratory or stationary strategy (left). The width if each bar is proportional to the square root of the sample size (number of deer) per study area. The error bars are the 95% bootstrap confidence limits. The mean deer density (shot per km^2) in the years of observation is presented as text in each bar. Pattern of seasonal migration along altitudinal gradients for 7 regions of Norway (right). Point estimates are the mean across individual females conforming to the seasonal migration strategy. Error bars are 95% confidence limits.

in female moose was triggered by snowfall (Van Moorter et al. 2013).

The decreasing proportion of migrants at higher density may suggests a role of social fences (Matthysen 2005). After the dispersal process, few deer alter migration strategy and/or home ranges between years (Sawyer et al. 2009; Middleton et al. 2013; Meisingset et al. unpubl). Deer typically show high fidelity to both their summer (Igota et al. 2004; Van Deelen et al. 1998) and winter ranges (Sweanor & Sandegren 1989), especially older animals (Aycrigg & Porter 1997). Further, females in several deer species tend to establish close to their mothers (Aycrigg & Porter 1997; Wahlstrøm & Liberg 1995). However, it might be that young deer trying to establish as migrants at higher density have more trouble finding areas without social fences, and therefore a stationary strategy might be a solution. A study of 20 years capture-mark-recapture data showed that the proportion of dispersing young males decreased with increasing density, but those dispersing increased the distance (Loe et al. 2009). This could likely be because it took a longer distance to reach low-density areas suggesting that social fences might be relevant for space use even in non-territorial cervids.

Insight into the processes determining partial migration can have marked implications for population dynamics (Kokko & Lundberg 2001) and therefore also for management and conservation of large herbivores (Milner-Gulland, Fryxell & Sinclair 2011). Our study highlight that several hypotheses can predict the same main pattern of altitudinal migration, and that predictions that are more detailed are therefore needed regarding timing, distance and patterns of partial migration. We suggest that a combination of avoidance of competition in high-density winter ranges, social fencing during summer in addition to the forage maturation and predation risk avoidance hypotheses, is needed to explain migration patterns of northern ungulates.

Migration – catching the green wave (PAPER IV)

Migration between distinct seasonal ranges is a widespread tactic among animals to adapt to spatiotemporal variation in resource abundance (Bolger et al. 2008). The typical pattern in herbivores at the northern hemisphere consists of seasonal movements between winter ranges at low elevation and summer ranges at higher elevation (e.g. Festa-Bianchet 1988), or migration to summer ranges further inland for coastal populations (Albon & Langvatn 1992). The FMH predicts that ungulates trade off forage biomass with forage quality in order to maximize energy intake and states that herbivores migrate along a phenological gradient of plant development in order to maximize energy intake over a prolonged period (Fryxell, Greever & Sinclar 1988; Albon & Langvatn 1992; Hebblewhite, Merrill & McDermid 2008). However, the more detailed relationship between plant phenology and ungulate movement has rarely been quantified, and consists mainly of qualitative support for the FMH (Hebblewhite et al. 2008). One more specific hypothesis attempting to link plant phenology and migratory movements more quantitatively is the green-wave hypothesis, a term first introduced in the waterfowl literature (Owen 1980). The hypothesis refers to the migratory phenomenon whereby birds (van Wijk et al. 2012) and now reported in ungulates (Sawyer & Kauffman 2011) follow a wave of spring toward their summer destination, leading to the expression “surfing the green wave”. There is a range of potential migration patterns in pursuit of the green wave. At one extreme, migrants slide across the landscape along with the leading edge of the green wave, whereas, on the other extreme, migrants move quickly between two main seasonal ranges, simply attempting to maximize access to high forage quality at each range. Between these extremes lie a number of possible green-wave pursuit patterns, one them represented by shorter steps frequently interrupted by stopovers.

In this study, we quantify the spatiotemporal relationship between plant phenology and the landscape-scale movement patterns of red, which should be particularly suitable because proportion of migrants varies substantially across the seven study regions (PAPER III). We developed a method for integrating satellite-derived vegetation indices (e.g. the normalized difference vegetation index, NDVI; Pettorelli et al. 2005b) with animal locations through a space-time-time matrix of phenology. In this matrix of resource state, one dimension represents geographical locations occupied during sequential time steps for the whole range of sites a given deer have visited and the second dimension represents the time series of resource state at each deer location. This approach allowed us to evaluate the consequences of both actual and hypothetical alternative space-use tactics. We used "springness" as the underlying quantitative measure of resource state. Because the rate of change in the NDVI has been directly linked to ungulate forage quality (Hamel et al. 2009), we define springness as the instantaneous rate of phenological green-up (Cumulative IRG). We linked plant phenology (MODIS–normalized difference vegetation index [NDVI] data) and space use of 245 (167 migratory and 78 resident) red deer of both sexes, using a space-time-time matrix of "springness" in 68 municipalities across our seven study regions (Figure 3). We tested a set of predictions based on the FMH and the green-wave hypothesis (for full list se PAPER IV).

We found that migrants experienced substantially higher access to springness (females: 33%, males: 24%) than residents did (Figure 9), qualitatively consistent with the FMH. Deer were also more likely to migrate in areas where migration led to greater gains in springness (Figure 10), and 85% of all migrants experienced a longer or more intense spring. However, most migratory red deer (78%) moved rapidly from the winter to the summer range (faster than spring green-up speed) thereby "jumping the green wave" rather than "surfing the green wave" (5%) during migration. The majority of migrants moved between distant winter and summer ranges in one or a few abrupt moves and used little time along the route (Figure 9B), thus not exploiting the full potential of the green wave. Although resident red deer in our study experienced reduced springness during the growing season, we found that they were still better off than migrants would have been if they had stayed at the winter range. We found an average of 18.5% compensation by female residents, compared with the predicted loss in springness that migrants would incur if they remained at the winter range and did not change their space use patterns. We found a positive relationship between springness and body weight for males, but not for females.

Evidence from our study was consistent with the qualitative predictions of the FMH, but in terms of quantity, they could have done better. Why is there a marked mismatch between

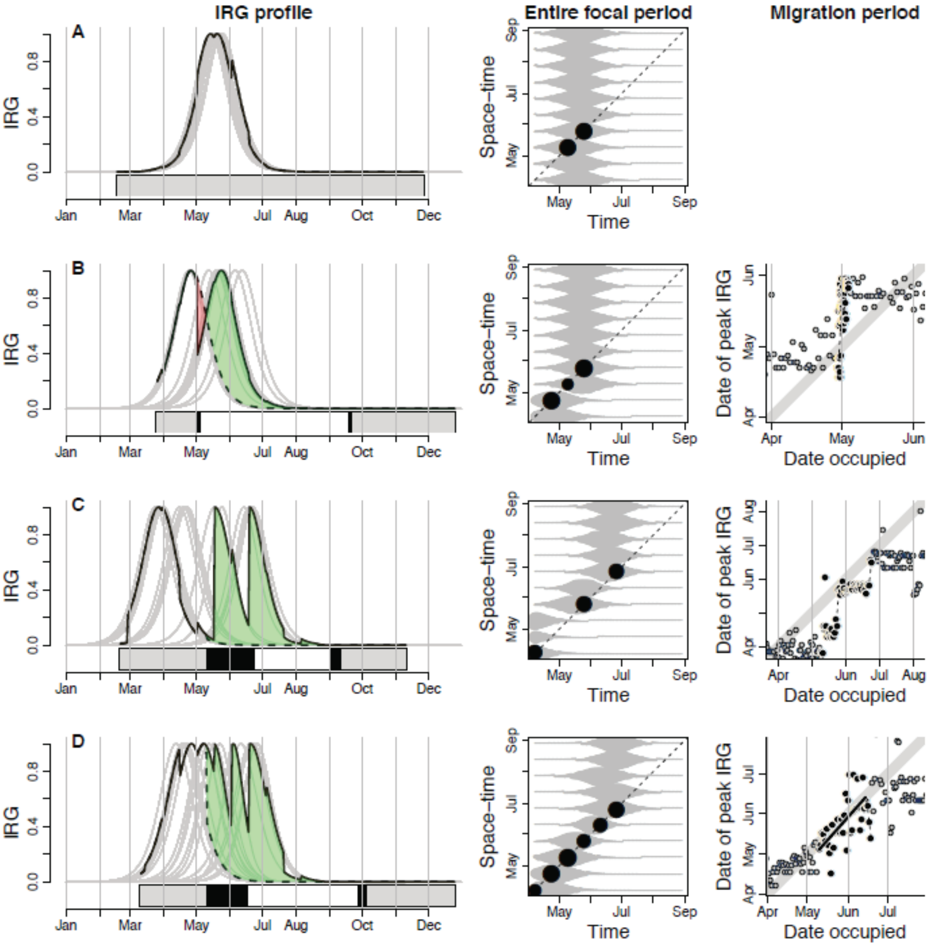

Figure 9. Patterns of springness (IRG) experienced by 1 resident (row A) and 3 migratory Norwegian red deer (rows B - D). (1) Plots on the left side show the IRG profile through the monitoring period. IRG time series associated with each location are shown as grey lines. The solid black line marks the IRG actually experienced by red deer throughout the monitoring period, and the dashed line marks the IRG pattern a deer would have experienced had it remained resident. Gains in cumulative IRG (ΔCIRG) because of migration are indicated with shading lines, losses with a solid grey fill (B). The horizontal bar at the bottom of the frame indicates time spent at the winter range (grey), during migration (black), and at the summer range (dark white). (2) Plots in the middle are a direct visual representations of the space-time-time matrix of IRG values. Time-series of IRG values for a given 16-day location cluster are shown as horizontal grey lines with the thicker segment corresponding to the spring green-up. These time series are arranged along the y-axis in order of occupation by the individual red deer. The diagonal represents IRG experienced at the time a location cluster was occupied, with black points where the IRG value is within 60% of peak IRG. (3) Plots on the right show the relationship between the date of peak instantaneous green-up at a given location and the date at which that location was occupied during migration (open circles: winter range, black dots: spring migration period, grey circles: summer range). The diagonal (thick grey line) represents the leading edge of the green wave and data points on the line are indicative of locations occupied at the time of their peak rate of green-up. The patterns shown for rows B, C, and D are indicative of jumping (A), jumping with stopover (B), and surfing (C), respectively. Regression lines are dashed, with the surfing segment shown in bold (D).

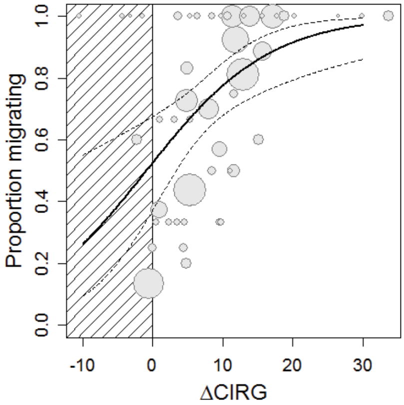

Figure 10. Proportion of red deer migrating in relation to the average gain in cumulative springness experienced as a result of migration. Individual data a are pooled by municipality in which deer were captured and marked, represented a circles. The relative size of the circles indicates the size of the sample associated with each municipality (N ranging from 1 to 16). Observations that fall within the shaded area represent municipalities where associated migrants, on average, experience a loss in cumulative springness. Predictions from a logistic regression model are superimposed, together with 95% CI boundaries.

plant phenological development along the migration route and the speed of migration of the typical Norwegian red deer? There may several the explanations of the phenomenon including 1) geographical discontinuity of resources or suitable habitats along the migration route (e.g. forage, shelter). It is likely that we can exclude this as a general explanation for the prevalence of jumping is our case, because we found that habitat suitability (mainly determined by forest cover; Loe et al. 2012) along the migration route was intermediate between that at the winter and summer ranges. 2) Reduced exposure to predators along the migration route. Many species are vulnerable during migration, providing incentive for faster migration to reduce exposure to risk (Festa-Bianchet 1988; Hebblewhite & Merrill 2007; Hebblewhite & Merrill 2009). Even though predators are absent or scarce in our study areas we cannot ignore the fact that many aspects of ungulate behaviour are shaped by predation in the past (Byers 1997; Bowyer 2004, see also discussion in PAPER III). 3) Timing and/or duration of migration may constrain life-history aspects beyond herbivory, such as calving. In our case, females typically give birth shortly after arriving the summer range (Loe et al. 2005), making it important to reach the summer range before a newborn calf restrict the mothers movements. 4) Competition for access to resources as foraging areas and shelter. Arriving early at their destination may be beneficial trait in competition with conspecifics, a common trade-off in birds (Kokko et al. 2006). This has also been suggested as a strategy in male roe deer, which are territorial during summer, and arriving earlier in their summer ranges than their female counterparts (Mysterud 1999). Whether animals without marked territoriality such as red deer can gain a competitive advantage from early or faster migration is less clear. However, in PAPER III, we suggested that the negative density dependence of the proportion of migrants might be linked to the social fence hypothesis, which has been offered as an explanation for population regulation and density-dependent dispersal in microtine rodents and birds (Hestbeck 1982; Matthysen 2005).

Our finding that proportion of migratory animals increases as the average benefit increases within an area, indirectly supported a possible fitness effect. However, the lack of an effect between springness on body weight in females may be explained by the constraints by having calves at heel (Bonenfant et al. 2004) or that females allocate extra energy to reproduction. However, both migrants and residents, tracked phenological green-up through the growing season by making small-scale adjustments in habitat use within their summer ranges. Resident individuals may adopt space-use tactics that allow them to partly compensate for the effects of not migrating (Hebblewhite, Merrill & McDermid 2008), maybe masking some of the effect of favourable spring condition.

Our analyses supported 3 out of 3 predictions for the FMH, but just 1 of 3 regarding the green wave hypothesis. However, we gained insights in how migrants track the rolling wave of vegetation green-up across the landscape, by investigating how individual red deer experience the green wave. Our study shows that the FMH is important in explaining the spring migrations across a range of populations; however, several hypotheses is needed to fully explain the space use patterns (PAPER III). In the light of climatic change, understanding the relationship between the green wave and ungulate space use pattern has important consequences for the management and conservation of migratory ungulates. For population managed through hunting, such as the red deer in Norway, is the seasonal range expansion in spring and range contraction in autumn, important to understand for future distribution of deer. The consequences of global warming are predicted to reduce the duration of snow cover in many area, but that the effect on snow will differ depending on altitude (Christensen et al. 2007). Therefore, a key issue is whether a given landscape would retain sufficient variation in snow accumulation to prolong the duration of the spring green-up under global warming, and thus the relative benefits of migration (Mysterud 2013). At lower altitudes, a warmer climate at a given latitude results in earlier onset of migrations and earlier reproduction in several taxa in temperate regions (Stenseth et al. 2002). However, contrasting patterns of higher temperatures have been found across altitudes. In western Norway, increasing temperatures and increased precipitation during winter resulted in less snow at low elevation and more snow at high elevation (Mysterud et al. 2000). Over a range of altitudes, lead this to increased spatial variation in plant phenology, and increased duration of spring across the landscape suitable for migratory red deer (Pettorelli et al. 2005a). By contrast, within two decades in Yellowstone, migratory elk experienced a faster and shorter duration of green-up coincident with warmer spring–summer temperatures and reduced spring precipitation consistent with observations of a severe drought in the region (Middleton et al. 2013). This landscape-level change in habitat quality, together with higher predation, appear to be responsible for the declining productivity of migrating animals in this population. Thus, the effect of changing climate conditions may differ across ecosystems and detailed study in several areas is needed to fully predict future effects.

Space use and scale of management (PAPER V)

Many large mammals have extensive annual ranges (e.g. Berger 2004) and population-level management is difficult to achieve for wildlife that routinely crosses administrative boundaries. Theoretical studies have documented that a more adapted management and a more optimal resource use can be achieved by collaboration over larger areas (Milner-Gulland, Coulson & Clutton-Brock 2000; Skonhoft et al. 2013). Management of wild populations should occur at population level if the aim is optimal resource use (Nilsen et al. 2009), but the "Convention on biological diversity" and the EU's Subsidiarity principle suggests management should occur at the lowest practical level (Linnell 2005). Delimiting functional population units are thus a difficult task (Singh & Milner-Gulland 2011; Bull et al. 2013), particularly in partially migration populations. Analysis of animal space use relative to administrative unit borders would be an important basis to suggest appropriate size of management units. Different trade-offs and spatial mismatches between management objectives and distribution of costs and benefits make delimitations particularly important.

In this paper, we combine data from 437 GPS-marked red deer across 7 counties in Norway (Figure 3) with information of the size and position of two different administrative levels, the governmental level (municipality) and the local management units (MU) to determine the scale of mismatch between biological and management units. We first analyse (1) landscape level predictors effect of proportion of migrators, timing and distance of migration, and home range size of male and female red deer. We then analyse (2) red deer space use patterns in relation to two administrative management levels (MU and municipalities) across populations differing largely in topography and other environmental factors. Lastly (3), we analyse how this affects the timing and likelihood of crossing management units.

The main landscape level predictor of propensity to migrate was diversity of altitudes. Propensity to migrate was higher in males than females and males migrated longer distances than females. Migration distance decreased with diversity of altitudes, and increased with latitude and proportion of forested areas. Distribution of annual home range size was bimodal because of the two main migration strategies, and for migrators related to mainly the same predictors as migration distance. For stationary deer it was positively related to proportion of pastures. At monthly scale had migrators far larger home ranges in May and September for both sexes, overlapping with migration periods. While individual annual range use clearly exceeded the spatial scale of MU's (39 % of female home ranges and 21 % of male home ranges), average municipality size was large enough to potentially contain 98 % and 94 % of female and male deer home ranges, respectively (Figure 11). However, even at this scale, when comparing migration distances with the diameter of the municipalities, it could potentially cover only 70 % of females and 62 % of males' yearly range. Only 12 % and 4 % of MUs were wide enough to encompass migration distances in females and males, respectively (Figure 11). Number of used municipalities was higher in migrating (37% used one; range 1-6) than stationary (86% used one; range 1-3) red deer, and males used more municipalities than females. Migratory deer used also a higher number of MU than stationary animals, and even if males used a higher number of MU than females during one season, was the effect of migration much larger than sex. While stationary deer of both sexes spent about 93% of their time in their core MU, migratory females spent 63.8 % and migratory males 56.5% of their time in one MU and spent most of the time (>86 %) in the one or two core MU. Timing of autumn migration was delayed with increasing diversity of altitudes, but individual timing of autumn migration was quite spread throughout autumn and 20 % of the deer of both sexes started before the onset the hunting season. Probability of crossing of management borders differed greatly between stationary and migratory deer, with migrating deer having higher probability to cross a border throughout the year (Figure 12). Migrating deer of both sexes show a bimodal distribution of the probability to cross borders, with males showing a higher crossing rate throughout most of the year.

The analyses of our extensive dataset across a considerable geographical range show that landscape level patterns are important for propensity to migrate, migration distances and home ranges sizes in red deer. A large-scale access to a diversity of altitudes was generally den most important factor for space use, as also shown in PAPER III and IV, which is also shown in elk (Hebblewhite, Merrill & McDermid 2008). Environmental factors were important in describing variable movement strategies in moose across a large latitudinal gradient in Sweden (Singh et al. 2012), whereas occurrence of migration in roe deer across Europe was a function of topography, climate and habitat characteristics (Cagnacci et al. 2011).

There has been an increasing body of literature regarding animal space use during the last decades, but surprisingly few attempts to link this movement data with applied issues of management scale (Linnell 2005). However, bioeconomic model shows that optimal harvesting rates and optimal population densities were affected by the migration rate in both moose and red deer. The differences between the unified and non-unified management schemes were minimal when migration rates were low, but became much more pronounced as the migration rate within the population increased (Nilsen et al. 2009; Skonhoft et al. 2013). Animal crossing of management borders may take place on different scales, from national borders between countries to crossing of boundaries between properties or MU. In Scandinavia, large carnivores such as wolves (*Canis lupus*) and bears (*Ursus arctos*) move regularly across national borders (Bull et al. 2009; Bischof & Swenson 2012). For cervids, movements are mainly at smaller scales, but the same issue of border crossings arises at local scales. The same biological population will be the target of various management regimes, for example can contrasting management goals between summer and winter ranges of deer have major effects on population development (Hebblewhite et al. 2006). We show that less than 40% of the females and about 25% of the males had a stationary space use and in particular migratory red deer used many MU during one season. We demonstrate that MU (the landowner scale) is excessively too small if the aim is population level management, while the municipality level is borderline by averaging a spatial extent sufficient to contain around 60% of all deer in a population. Together with extensive border crossing, especially during migration periods, this challenge today size of MU, thus the spatial scales for management. Coordination across MU in the size and composition of quotas may potentially decrease the need for larger MU as coordination may make effective MU size to be larger. However, management goals and harvest patterns often differ quite a lot across units depending on local conditions for both cervids (Gordon, Hester & Festa-Bianchet 2004; Milner-Gulland, Coulson & Clutton-Brock 2004) and carnivores (Bischof et al. 2012). In our study area, there was considerably differences in both in the absolute number and composition of harvest at both the level of MU and municipality (Meisingset et al. unpubl.), which potentially have great effect on the population growth rate (Langvatn & Loison 1999).

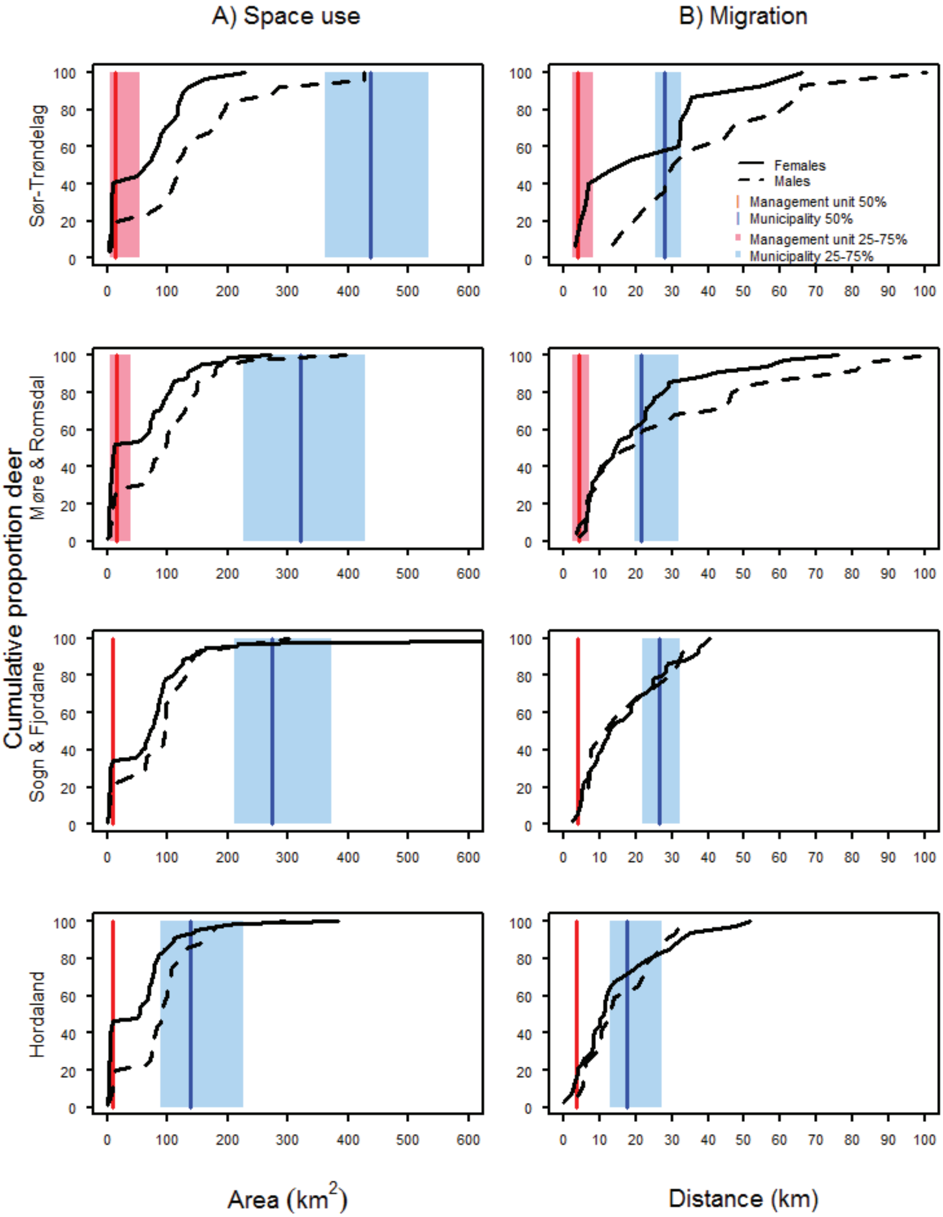

Figure 11. Space use (annual home ranges; A) and migration distances (B) showed as accumulated proportion of each sex (solid line=females, broken line=males) in relation to area (km²) and diameter (km) of management units (MU; red) and municipalities (blue) in different 4 different study region (N=Sør-Trøndelag, NW=Møre & Romsdal, W=Sogn & Fjordane, SW=Hordaland) . Red and blue lines represent the median area (A) and diameter (B) of the units, and the coloured area the 25% and 75% quantiles. In Sogn & Fjordane and Hordaland we had just access to medium areas of MU (i.e. no quantiles are available).

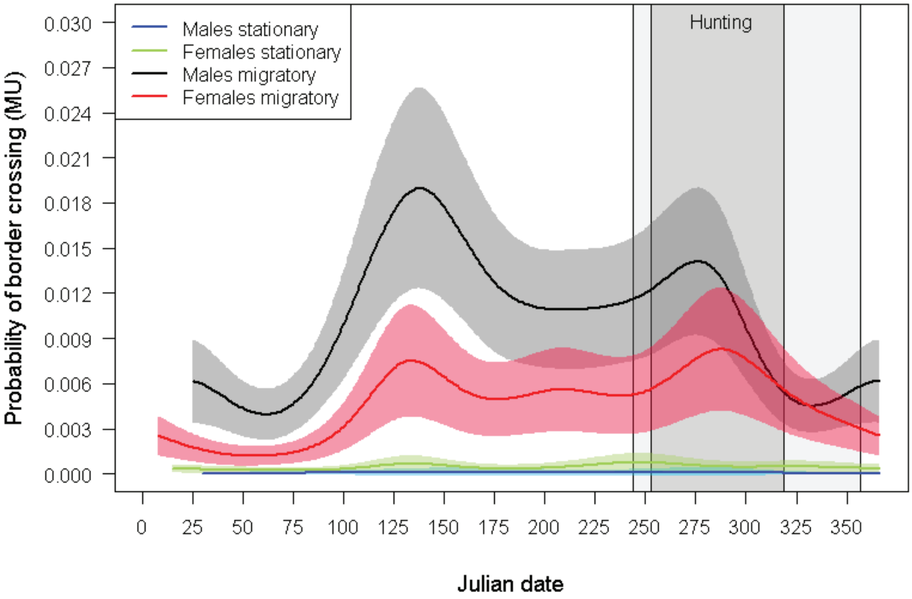

Figure 12. Probability of border crossing of management units (MU; per hour) as a function of Julian date for stationary and migratory red deer of each sex. Lines represent predicted effects from a GAMM. Colored shaded areas corresponding to line color represent confidence polygons of the predicted effects. Light grey shaded area represent the present hunting period, whereas the darker grey area represent the former hunting period (see methods).

In our study, males showed greater tendency to migrate, migrated longer, had greater home ranges than females and resulted in more MU used and higher crossing frequency of management borders than females. In a situation where space use in males exceeds females, and are spatially segregated on a larger scale, there may be a large risk that the over-exploitation of males because they a target for hunting at larger spatial scales (Jarnemo 2008). Over-exploitation of males is common in many areas (e.g. Solberg et al. 2000), which may have negative effects on the population (Mysterud, Coulson & Stenseth 2002). To account for large distance movements of male red deer in Slovakia, the minimum extent of hunting ground is 20 km² (Kropil, Smolko & Garaj 2015), whereas such management regulations are rare in other European countries (Putman, Apollonio & Andersen 2011). Management may fail because of different hunting regimes and competition over mature males between hunting units, even if space use patterns are well known (Clutton-Brock et al. 2002).

The analyses of the MU border crossings showed that the frequency peaked during migration periods, and in the autumn migration did 80% of the migrating deer movements overlap with the hunting season. The hunting season of cervids varies widely across Europe (Apollonio et al. 2011), and provide potentially an important tool to redistribute harvesting of migratory populations. In Norway, there has been an extension of the hunting period during the last decades, the hunting period starts earlier and last longer, which may have consequences for hunting mortality and distribution of harvest. The implementation of a longer hunting season led to a higher harvest of late migrants in elk in Wyoming in USA (Smith 2007), whereas in Norway an earlier start of the hunting season has led to relatively larger harvest at higher altitude units (i.e. summer ranges; Loe et al. unpubl.).

Managers should be aware at which spatial level they manage populations. Space use of many ungulates is closely linked to large-scale landscape characteristics and habitat features, and GPS studies can be an important tool for assessing proper spatial scales for management in different environments. Our results show that existing MU are far too limited to be able to manage a population as one potential unit, and even municipalities are too small when considering migration distances.

Habitat and distribution of harvest (PAPER VI)

Many cervid populations in Europe and North America are managed through selective harvesting, and the way this is implemented has a huge impact on population growth rate (Solberg et al. 1999; Milner et al. 2006). Most of the selectivity arises due to management regulations such as age- and sex-specific quotas (Mysterud 2011), but hunter preferences also play a role, especially for trophy hunting (e.g. Coltman et al. 2003; Martinez et al. 2005). Recently, it has been highlighted that harvesting selectivity may arise indirectly through animal behaviour, for instance if animals make themselves more or less prone to harvest by the use of open habitat (Ciuti et al. 2012). Weather conditions can affect behaviour, influencing both small and large-scale movement of deer (Rivrud, Loe & Mysterud 2010) and thus affecting their likelihood of being targeted for harvest. Here, we use red deer to explore how habitat characteristics affect the behavioural decisions of the animals and their hunters throughout the hunting season. Due to access to uniquely detailed data, the Norwegian red deer population is a useful model system to investigate how habitat types (farmland vs. forested habitat) affect hunter effort and harvesting off-take, and how this varies with age and sex class. The basis for quantifying these interactions are data on habitat type at the culling site and date of culling of harvested animals and daily data on hunter effort of red deer in Norway.

The probability of being harvested on farmland decreased as the hunting season progressed (Figure 13a). We found a small effect of age, with calves having a higher probability of being harvested on farmland late in the season, and a non-significant trend toward younger animals (yearlings) having a higher probability of being shot on farmland early in the season. Yearlings showed largest variation in the probability of being harvested on farmland, but there was no effect of sex. All ages showed a higher probability of being harvested on farmland when there was a rutting break, than when there was no rutting break in the hunting season, and the magnitude of the increase depended on age. Although weather played a measurable role, the effect of moon phase was a stronger predictor of the probability of being harvested on farmland. Moonlight became progressively more important in mid- and late hunting season (Figure 13b). Hunter effort declined through the hunting season. Hunter effort was significantly higher during weekends, and the difference increased through the season. Hunter effort and total harvest number increased during full moon periods compared to new moon, but only in the mid – and late season. Overall harvest numbers declined through the season and there was a strong positive effect of hunter effort on total harvest numbers. The proportion of quota filled was positively associated with harvest numbers throughout the season, which indicates that quota was not a limiting factor for harvest in most hunting areas.

Habitat characteristics have been shown to affect predation risk in ungulates and success for their predators (e.g. Kunkel & Pletscher 2000; Lone et al. 2014). Hunting is the main cause of mortality in many managed ungulate populations (Langvatn & Loison, 1999), and they should therefore avoid humans in space and time. Elk were more likely to be shot during hunting if they selected open areas, used flatter terrain and had higher movement rate (Ciuti et al. 2012). Further, this study showed that older and more experienced females decreased detectability by moving slower, avoiding open areas, and consequently they all survived the hunting season, suggesting a learning effect with age. In a recent study of red deer, the onset of hunting induced an immediate switch to habitat with more concealing cover in surviving males, but not in males that were later shot (Lone et al. 2015). However, in females no such relationship was found. In moose, males exposed themselves more often to the hunters than females did (Solberg et al. 2010), making them more vulnerable for hunting mortality. In the monomorphic red grouse (*Lagopus lagopus scoticus*), sex- and age-specific behavioural differences caused differential vulnerability to harvesting and a larger off-take of young animals at large bag sizes

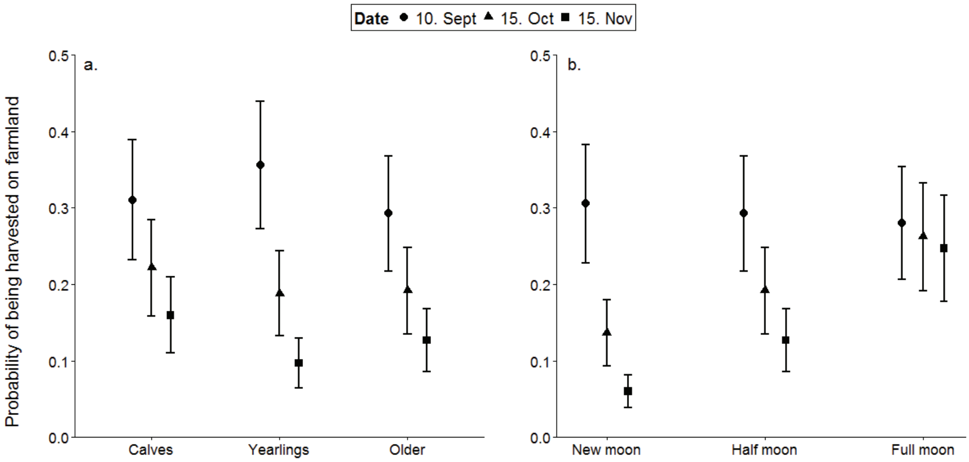

Figure 13. The probability of red deer being harvested on farmland through the hunting season, ± SE, for a. different age groups and b. different moon phases. Circles: 10. September; triangles: 15. October; quadrates: 15. November. Estimates are based on a generalized linear mixed-effects model for binomial data with municipality and year as random intercepts and N_{obs}= 19769. The fixed effects not investigated in the plot were held as follows: temperature = mean, precipitation = 0, age = adults, moon fraction = half-moon and rutting break = no.

(Bunnefeld et al. 2009). Following this, should young inexperienced deer, especially males; have a higher probability of being harvested in open habitats like farmland.

We did not find any differences between the sexes, but calves had the highest probability of being harvested on farmland late in the season, and there was a tendency for the same pattern for yearlings early in the season. Toward the end, yearlings had the lowest probability of being harvested on farmland, perhaps indicating that learning is already taking place. Many species are known to shift their habitat use into safer habitats in response to human disturbance (Frid & Dill 2002). Lowered hunting activity during the rutting break could therefore lead the deer to increase their use of open, risky habitats. A higher number of animals may then be available on farmland when the hunting resumes after the break, thus increasing the harvesting probability in the habitat. Moreover, deer that use safer forest habitat might survive better because they make safer choices in general. Altogether, this suggest that predictable harvesting regimes with high harvest rates could create a selective pressure for deer to respond dynamically to the temporal change in hunting risk.

We cannot ignore effects of how hunter preferences change during the season or the pattern can arise due to depletion of yearlings. Hunters often seek to harvest the yearling quota early in the hunting season, as they then are easier to separate from older (and younger) animals. In addition, hunters are expected to be less choosy toward the end of the hunting season in order to fill their quotas. This behaviour might yield unintentional harvesting selection, as is the case for red grouse (Bunnefeld et al. 2009). Unintentional selection of specific age or sex classes can lead to decreased population yield at high harvesting rates (Bunnefeld et al. 2011b). Hunters can differ largely in their effectiveness depending on their motivations (Andersen et al. 2014), and hunter behaviour through different methods (Martinez et al. 2005) or categories of hunters (Rivrud et al. 2013) can influence the composition of the harvest. Key components often recognized when considering sustainability in harvested systems are the life history of the species and the management objectives (Johnston, Arlinghaus & Dieckmann 2010), while hunter behaviour is often ignored when formulating guidelines. The importance of including behaviour for understanding human harvesting has been acknowledged as an important basis to achieve sustainable management of recreational fisheries (e.g. Hunt et al. 2011). This subject is likely to become increasingly important also in deer management, now that deer numbers are increasing in Europe while the number of hunters is decreasing (Andersen et al. 2014).

The effect of hunter effort on total harvest numbers was also dependent on temperature and moon phase, again showing how many factors interplay in determining patterns in harvesting. Knowledge about heterogeneity and dynamics among hunters and their corresponding variation in hunter preference should therefore be incorporated when formulating management rules. Such insight can be used in order to influence hunter behaviour in such a way as to change the sex ratio and/or age distribution of the harvested populations, for example through different price categories or monitoring of hunter behaviour which can be implemented into management guidelines.

General discussion and conclusions

Movements of animals concern the management of their population. Different species have diverse spatial patterns, from the migratory wildebeest that cover large areas to species that spend their life cycles within small areas. Knowing animal movements is one criterion that managers should care about, because it has vital effect on density, distribution and harvest of populations. GPS technology in ecological studies has opened a new world of possibilities to study animal space use (e.g Cagnacci et al. 2010; Mysterud 2013), a technology I have utilised throughout my thesis. I have demonstrated that red deer use larger areas than the extension of management units, and thus identified a mismatch between management units and animal space use. This spatial mismatch can give several challenges to the management. First, allocation of quotas and definition of hunting period need to take migration pattern into account to optimize the harvest yield (Nilsen et al. 2009; Skonhoft et al. 2013). Second, knowledge of shared populations is the first step to start developing unified management regimes across current administrative boundaries (Linnell et al. 2001). This might be easy to imply in some areas, where there already is common goals for population development and harvesting regime. Importantly, the main challenge is to reach consensus for a unified strategy among neighboring areas diverging in terms of inflicted damage by deer and benefit from hunting and harvesting regime. The next question is then: who should collaborate and/or unify? To answer this, the next step will be to develop spatial models identifying areas likely to share a population. Only then will managers have to tools to implement acts, as for example distribution of hunting quotas more precisely. I have provided a foundation for this future work, by unravelling the spatial extent of current movements and the ecological drivers of migration providing a framework for predictions.

One of the largest anthropogenic influences on ecosystems of our times are increasing human infrastructures such as roads (Foreman & Alexander 1998). Roads can affect large herbivore population directly by inducing mortality or indirectly if acting as barriers to movements or if animals avoid roads. The main effect of roads to red deer is the direct effects of mortality, which may be substantial (Mysterud 2004). Use of open agricultural pastures is frequent in red deer because of favourable foraging conditions (Godvik et al. 2009). Road crossings are thus likely to be motivated by directed movements to access pastures (Gagnon et al. 2007). It is therefore important to understand why and where deer cross roads, and how management can affect the likelihood that road crossings do not lead to an accident. In my thesis, I focussed on the patterns avoidance and crossing frequency of roads in red deer (PAPER

I) and which factors influence the collision risks at the within-home range scale (PAPER II). Ungulates may avoid roads for several reasons; including the road itself, the opening a road creates, human disturbance, and the vehicle traffic. In our study was avoidance behaviour weak and crossing frequency high (PAPER I), which indicate that roads had no severe implications for carrying capacity and did not cause obstruction for daily and seasonal movements. However, in our case, the total road density was quite low (0.37 km/km^2), and we cannot rule out a more severe indirect effect of roads when road density is higher. Human access and disturbance effects on remote areas tend to increase with higher road density (Rowland et al. 2000), and habitat loss occur when road density exceed a certain threshold (Frair et al. 2008). A road density of about 0.6 km/km^2 appears to be the maximum for a naturally functioning landscape containing sustained populations of large predators, such as wolves (*Canis lupus*) and mountain lions (*Felis concolor*; Foreman & Alexander 1998). In elk, a road density of 1-1.5 km/km^2 had effect of mortality risk and dispersal patterns (Frair et al. 2008). Even if road density or anthropogenic features increase within an area, red deer likely will follow their traditional routes (Sweanor & Sandegren 1988; Andersen 1991). Indeed, crossings occur more often in dense forested habitats and close to pastures (PAPER I). In addition, DVC risk was also higher close to pastures (PAPER II), which make these areas suitable for mitigation measures. In line with this gave an experimental vegetation clearance along a highway within our study area a significant reduction in collision frequency (PAPER II). Since DVC risk was higher in darker periods of the year and increased with speed limit and productive forest cover (PAPER II), is the human driver effect an important factor when considering mitigation measures to prevent DVC. Efforts which make drivers able to detect deer when they are approaching the road, and/or measures to reduce the stop length of vehicles, should then be effective to reduce risk for DVC. Even though reducing speed limit may be unpopular as a mitigation effort, it is probably effective to reduce DVC risk, especially in risk zones close to pastures. Together with vegetation clearance along the edges of roads, this will be effective tools for reducing risks for DVC. When targeted at shorter road stretches with high DVC frequencies it will probably also be a cost effective mitigation measure in many areas.

The movement of thousands of animals across large spatial scales on a seasonal basis is among the most spectacular and a well-recognized phenomenon of the natural world (Milner-Gulland, Fryxell & Sinclair 2011). These movements have fascinated and inspired natural researchers for a long time and a large amount of research effort has been invested into understanding the causes and consequences of migratory behaviour across the animal kingdom. Several environmental and landscape scale factors determining migration and space use patterns has been identified in this thesis, and how they relate to current management scales. Proportion of migrating red deer increases with a variable topography and access to high altitude habitats (PAPER III, PAPER V), and in areas with greater gain in springiness (PAPER IV). In line with this are summer ranges located at higher altitudes (PAPER III) and migration distance decreases with access a variable topography (PAPER V). The makeup of these drivers of migration determines the ability of migratory populations to adapt to changes to the spatiotemporal arrangement of resources. In PAPER IV we show that migrants gain increased springiness and there is clear evidence that ungulates benefit qualitatively from migration (Hebblewhite, Merrill & McDermid 2008). However, our study suggest they could do even better, because the red deer move quickly between the winter and the summer home range; they are green-wave jumpers at a coarse scale (PAPER IV). During migration, small-scale foraging decisions may be overruled by other decisions operating at larger scales (Mysterud 2013). Deviations from optimal surfing of the spring green wave may be due to trade-offs between energy intake and predator risk (Festa-Bianchet 1988; Hebblewhite & Merrill 2009) or other constraints on space use such as avoidance of competition in the winter range (PAPER III). Even though migration is shown to be favourable in terms of prolonged access to favourable foraging conditions (PAPER IV), some individuals remained stationary in their winter range (PAPER III; PAPER IV; PAPER V), as shown in other populations with migratory ungulates (e.g. Hebblewhite, Merrill & McDermid 2008). Also, proportion of migrants vary between populations, and are related to population density at winter ranges (PAPER III). This suggests that several mechanisms to be involved when individual adopts their space use tactic. However, resident individuals partly compensate the loss in springiness by small-scale movements within the resident home range and thus surf on a wave of plant green-up beyond the migration period (PAPER IV). In addition, stationary individuals with larger access to agricultural pastures at a landscape level had larger annual home ranges (PAPER V). It is suggested that agricultural subsidies and access to pastures could favour a non-migratory space use strategy (Middleton et al. 2013; Mysterud 2013). Frequently use of agricultural pastures as shown for red deer (Godvik et al. 2009; Zweifel-Schielly et al. 2012), with several peaks in forage quality during the summer period due to grass harvest, may partly explain that both migratory and stationary space use strategies persist in the same population because the relative benefit may vary over time. Knowledge of factors that is crucial for individual migratory strategies and why both a resident and a migratory strategy co-exist will be increasingly important when managing populations in the future (Mysterud 2013). Indeed, we still have few studies documenting the fitness of stationary and migratory animals in partial migratory populations (Hebblewhite & Merrill 2011), and this remains clearly important for future work.

Across Europe, a widespread sustained harvest growth has occurred in several ungulates, such as in red deer, suggesting continued growth of many populations with biological, social and economic impacts (Milner et al. 2006; Apollonio, Andersen & Putman 2010; Putman, Apollonio & Andersen 2011). However, management strategies, hunting objectives and environmental conditions varies significantly between and within countries. Population control is therefore a major challenge for the future, currently hampered by inadequate population data, a decreasing number of hunters and possibly also by cultural traditions (Milner et al. 2006). To date, the management of ungulate populations has tended to focus on the management of single populations within defined management units (MU), for example estates, community lands and nature reserves/national parks. The management of many these wide spread ungulate species is likely to be influenced by the fact that animals move across management unit boundaries, who may hold contrasting management objectives (Gordon, Hester & Festa-Bianchet 2004; Nilsen et al. 2009). In PAPER V, we show that red deer use several MU during the year and that especially migratory deer frequency crosses management borders. Taken the annual space use of red deer into account is both the MU level and the municipality (governmental) level too small to maintain a population level management. In a situations with spatial variation in proportion of migrant and migration distances, as in our case (PAPER III; PAPER IV; PAPER V), will costs (damage) and benefits (harvest income) vary among landowners. Harvesting regime and therefore population density may be affected by the narrow self-interests and degree of coordination between MU/landowners (Skonhoft 2005; Nilsen et al. 2009; Skonhoft et al. 2013). Management of species like red deer at proper spatial scales may be a challenge because the costs and benefits are asymmetrically distributed in space due to migration (Skonhoft 2005; Skonhoft et al. 2013). Thus, it would be easier to distribute proportionally cost and benefits within one management unit (Skonhoft et al. 2013). Further, if neighbouring MU have very different goals (e.g. hunting and conservation; Hebblewhite et al. 2006; Singh & Milner-Gulland 2011), management may fail with large impact on population growth rate. In addition, in situations where space use of males exceeds females as in our case (PAPER V), competition over mature males among hunters may lead to over-exploitation (Clutton-Brock et al. 2002; Jarnemo 2008) and possible long term negative effect of population viability (Mysterud, Coulson & Stenseth 2002). In the future, MU should more closely reflect the biology of the populations rather than the human-defined ownership and jurisdictional boundaries, and be coupled with policy and management instruments that facilitate the co-operative management of large herbivore populations. Even though it might be difficult to delimitate sub-populations in partially migration population with more or less continuous large-scale spatial continuous populations, larger spatial areas will share larger parts of a population. From an ecological point of view, incorporating animal space use into harvesting would be important if the sub-populations are linked by migration or dispersal, because management actions taking place in one patch will generally have an effect on the population processes in the other patch, and vice versa (Gordon, Hester & Festa-Bianchet 2004). Thus, a framework how to demarcate functional management units for partially migratory populations' should be important in the future.

At both small and large scale, weather conditions and animal space use may interact in determining harvesting vulnerability and hunter selection. In PAPER VI, we show that probability of being harvested in open habitats decreased as the hunting season progressed and young animals showed the highest variation. The effect of autumn weather conditions and harvest effort and numbers varied through the season. The effects of weather on the probability of being harvested on farmland were in many cases consistent with the common knowledge of use of cover (Mysterud & Ostbye 1999). Use of covered and open habitats consistent with anti-predator behaviour during moonlight nights, and learning effects may play a role for age specific harvesting vulnerability in open habitats (Lone et al. 2014; Lone et al. 2015). The interactions found between weather, space use and animal and hunter behaviour indicates that further studies should enable a deeper understanding of the intricate interactions influencing vulnerability and selection in harvested populations. The study is among the first to highlight that weather may affect harvesting patterns and off-take indirectly through animal and hunter behaviour, but the interaction effects of weather and space use on hunter behaviour are complex. Future studies should therefore seek to understand the dynamics of hunter behaviour, how this can be influenced, and utilize this in the interplay between hunters, animal space use and management rules to obtain sustainable off-takes in managed populations.

To sum up, my thesis provide novel insight about the behavioural mechanisms underlying space use on different spatial and temporal scales by analysing data from an extensive dataset of GPS in red deer. Understanding mechanisms, and not only report patterns, is the key to predict under various environmental conditions. Knowledge of animal space use gained in my thesis may provide new insights and hence benefit management of many species and ecosystem. I show that roads affects red deer behaviour, but just at small scales and the risk of DVC is related to factor such as speed limit and access to pastures, and vegetation clearance lowers DVC risk in targeted road sections (PAPER I; PAPER II). Further, migrants experienced substantially higher access to springness, quantitatively supporting the FMH, but most deer moved rapidly hereby “jumping the green wave” rather than “surfing the green wave” during migration thus not fully utilize the potential during the green up (PAPER IV). The variable migration patterns (e.g. proportion of migrants) needs several hypotheses to be explained, including the competition avoidance and social fences hypothesis (PAPER III). The annual home ranges in both sexes, and especially among migrants, exceeded considerably the size of management units and questions the spatial scales of current management (PAPER V). Lastly, the thesis show that hunting vulnerability on open habitats differed throughout the hunting season, but total quotas seem more important for off take than hunter preferences and behaviour (PAPER IV).

Deer populations provide important revenue to local economies, yet their current population density in many areas create challenges to agriculture, forestry and road collisions. Clearly, regulation of population density will remain a key issue for future population management. My study highlight that knowledge of space use is important. With current global change of both land use and climate, it is likely that these issues will become even more important in the future. With this in mind, will cooperation and interaction across structures likely be a key issue for future population and ecosystem management. A unified management will be crucial to how our populations can be sustained in the modern world where both animals and humans has their natural place.

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