Space use, climate and selective harvesting of red deer

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Dissertation presented for the degree of

Philosophiae Doctor (PhD)

2013

Centre for Ecological and Evolutionary Synthesis

Department of Biosciences

Faculty of Mathematics and Natural Sciences

University of Oslo

Series of dissertations submitted to the
Faculty of Mathematics and Natural Sciences, University of Oslo
No. 1343

ISSN 1501-7710

Cover: Inger Sandved Anfinsen.
Printed in Norway: AIT Oslo AS.

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PREFACE

First of all, I would like to thank my supervisors. I am in great debt to my main supervisor, Atle Mysterud, whose door was always open to me and my endless chatter and concerns, sometimes, maybe to his annoyance, several times a day. Your incredible knowledge about ecology and your ability to give me swift responses with greatly improved drafts and clear answers to imprecise questions never seizes to impress me. In addition, you've taught me invaluable things about bikes, cross-country skiing and practical jokes. Leif Egil Loe, having the privilege of sharing an office with you in the beginning of my PhD really gave me a kick-start, both with regards to my work, and to knowing the latest gossip. Your ability to think of less complicated ways to do my in general unnecessarily complicated analyses has indeed broadened and upgraded my statistical knowledge. And finally, Geir O. Storvik – It's been a great help to be able to turn to you for help when I got stuck with the really tough statistics.

I wish to thank Erling L. Meisingset for letting me join in on red deer marking in Tingvoll, and thus get some up close and personal contact with my study species. Jon Olav Vik, thanks to the endless statistical discussions and your great help, you really improved paper I. Great thanks go to Sándor Csányi, for letting me take part in the Hungarian hunting culture, which is very different from what I'm used to in Norway. I'm also very grateful to all people who have assisted in the marking of red deer in the various Norwegian municipalities, and made data material available for this PhD.

To all my good colleagues at CEES: Thank you for providing an inspiring environment with never-ending knowledge about a wide range of topics. Special thanks go to Anders N. for giving me several breaks from work, even when I didn't know I needed them, and to Annette, Kjetil, Jo, Lars, Anders H. and occasional drop-ins for great lunches.

Finally, this work would not have been wrapped up in this book without the help and support of my family. You have encouraged me and supported me all the way, and also made me think of non-PhD-related things when needed. To my dear husband, Jostein: thank you for always being there for me. You've enriched my everyday life, always encouraged me and helped me bring my work further.

Blindern, February 2013 – Inger Maren Rivrud

CONTENTS

ABSTRACT

Cervid populations in Europe are hunted for a range of different purposes, such as meat, trophies or population control, but are commonly managed through some kind of selective harvesting. Examples of harvesting selection due to management rules (age- and sex specific quotas) and hunter preference (often size-specific) are fairly well-known, while there is less knowledge about how differential harvesting vulnerability due to individual animal behaviour affects harvesting selection in ungulates. Space use in ungulates is influenced by a wide range of factors such as climate and habitat characteristics, and these factors may operate differently depending on the age and sex of the individual, and on different temporal and spatial scales. Knowledge about how environmental factors influence activity on different spatiotemporal scales and hence also harvesting vulnerability is important to gain a deeper understanding of harvest selection patterns and how to implement management rules. Understanding habitat selection and space use is also important in itself to advance a general understanding of the species. The main aim of this thesis is to identify the underlying behavioural mechanisms determining space use in red deer (*Cervus elaphus*) on different spatial and temporal scales, and relating this to climatic variables, habitat characteristics and in turn how it may affect hunter selection.

Factors influencing space use and harvesting selection in red deer was studied in a population of red deer covering the core distribution range on the west coast of Norway, with a combination of data from GPS- and VHF-collared individuals and from harvest statistics. In addition, harvest records from Hungary on red deer males, including more than a century of data, was used to compare between hunting cultures, to look at patterns of hunter selection in space and time and long-term trends in antler size. Hypotheses on habitat selection and space use in Norwegian red deer were tested in paper I, where the use of open and covered habitats in relation to climate and plant production, and how this varied with activity/time of day and seasons was used to identify potential trade-offs resulting from anti-predator behaviour. Hypotheses regarding the home range scale was tested in paper II where I compared different temporal scales to disentangle how direct (thermoregulatory) and indirect (plant production) effects of climate affected red deer behaviour. I used the knowledge gained in these two papers to investigate how interaction effects between local weather and space use influenced harvesting vulnerability and hunter effort in paper III. Finally, in paper IV I used the

Hungarian red deer population to explore spatiotemporal patterns in hunter selection and to identify potential undesirable long-term consequences of trophy harvesting.

Patterns of habitat selection depended on activity and time of day, suggesting a trade-off in selection of open (risky, but rich in forage) and covered habitats (safe, but with less forage). Pastures were frequently used during darkness when activity was high, while forested habitats were used to a higher extent during daylight, the typical resting/rumination period. Red deer with low availability of pastures in their home range showed high selection for this habitat, but selection decreased when availability of pastures increased. This is termed a functional response in habitat selection, and probably resulted from anti-predator behaviour. The strength of the functional response varied with season, in relation to the expected distribution of available forage in covered and open habitats. Home range size increased when temperatures were higher than normal during winter, and decreased with higher temperatures during summer, across all temporal scales. The effect of precipitation was less clear, except when accumulating as snow. Snow depths deeper than normal lead to decreased home range size across all temporal scales. The effect of climate was stronger on long (biweekly-monthly) than on short temporal scales (daily-weekly), indicating that indirect effects of climate operating through plant growth had a stronger influence on home range size than direct climatic effects. When investigating effects on harvesting vulnerability directly, I found a pronounced effect of temperature on the timing of migration. The relationship between fall weather conditions and harvest numbers, hunter effort and risk of being harvested on farmland was highly variable through the season. Moon phase and day of week were the strongest predictors of harvesting risk and hunter effort, with higher effort, harvest numbers and higher risk of being harvested on farmland during moonlit nights, and higher effort and harvest numbers during weekends. Young, inexperienced animals had an increased risk of being harvested on farmland early in the season, but there was no effect of sex. Finally, we found large spatiotemporal variation in hunter selection in Hungary, when comparing foreign trophy stalkers and local hunters. Long-term trends in trophy size (1881-2008) showed no overall decline, and the pattern observed was consistent with changes in age structure due to periodically high harvesting pressure, and not with depletion of genes resulting in an evolutionary response. Environmental effects such as climate, land use change and density dependence can however not be excluded as contributors to the pattern observed. Future studies should therefore continue monitoring and strive to collect data on genetics and environmental factors to identify other potential drivers behind antler size development.

LIST OF INDIVIDUAL PAPERS

This PhD thesis is based on 4 papers. They are later referred to by their Roman numerals.

I. Godvik, I. M. Rivrud, Loe, L. E., Vik, J. O., Veiberg, V., Langvatn, R. & Mysterud, A. (2009) Temporal scales, trade-offs, and functional responses in red deer habitat selection. *Ecology,* **90,** 699-710.

II. Rivrud, I. M., Loe, L. E. & Mysterud, A. (2010) How does local weather predict red deer home range size at different temporal scales? *Journal of Animal Ecology,* **79,** 1280-1295.

III. Rivrud, I. M., Meisingset, E. L., Loe, L. E. & Mysterud, A. Interaction effects between weather and space use on harvesting effort and -selection in red deer. Submitted *Journal of Animal Ecology*.

IV. Rivrud, I. M., Sonkoly, K., Lehoczki, R., Csányi, S., Storvik, G. O. & Mysterud, A. (2013) Hunter selection and long-term trend (1881-2008) of red deer trophy sizes in Hungary. *Journal of Applied Ecology*, **50**, 168-180.

INTRODUCTION

Humans have always exploited a wide range of animals for important resources, such as food and nutrition or materials for manufacturing of tools and clothing. Cervid populations in Europe and North America are hunted for the sake of meat, recreation, trophies, or for population control (Gordon, Hester & Festa-Bianchet 2004; Apollonio, Andersen & Putman 2010). Populations are generally managed through some form of selective harvesting, and management rules are often based on age- and sex specific quotas (Mysterud 2011). In many countries hunter preference for large size is present, and this is particularly strong in populations experiencing trophy harvesting (Coltman *et al.* 2003; Garel *et al.* 2007). Harvesting is thus a non-random process imposing varying selection pressures on the population, either through age- and sex specific quotas as found in many ungulates (Langvatn & Loison 1999; Solberg *et al.* 2000), or through size selectivity as found in fisheries and trophy harvesting (Coltman *et al.* 2003; Olsen *et al.* 2004). Selection patterns induced by human harvesting often oppose the natural selection patterns, and may be strong enough to cause undesirable life-history trait changes over much shorter time spans than expected from natural selection (Coltman *et al.* 2003; Carroll *et al.* 2007; Garel *et al.* 2007). In ungulates, most attention has been paid to populations experiencing trophy harvesting. In these populations directional harvesting selection is particularly strong, as hunters actively remove the largest trophies and thus target the traits they actually desire. Also, populations where a decrease in trophy size has been reported are small and isolated (Coltman *et al.* 2003; Garel *et al.* 2007), which may contribute to an even faster evolutionary response towards smaller trophy sizes.

The potential for unintentional directional selection arising from individual animal behaviour and space use has received less focus. Recently, animal behaviour has been found to influence the risk of being harvested through space use in brown bears (*Ursus arctos*; Bischof *et al.* 2009) and red grouse (*Lagopus lagopus scoticus*; Bunnefeld *et al.* 2009). Knowledge about behaviour and harvesting vulnerability is scarce, but is likely to be an important factor influencing harvesting selection in ungulate populations. When looking at changes in phenotypic traits, less attention has been paid to larger populations, populations with other harvesting cultures than trophy harvesting, and long-term (century-scale) monitoring of populations experiencing trophy harvesting. Space use and habitat selection are important components of the ecology of species, and gaining deeper knowledge about these topics is important in itself to advance a general understanding of the species. This thesis therefore aims to identify the underlying mechanisms influencing space use through animal behaviour, and subsequently explore how this can affect harvesting selection. With the recent advances in technology, detailed monitoring data on movement and animal behaviour is available through GPS-equipment. Also, data on environmental variables such as climate data and habitat characteristics are more readily available. Most classical studies on animal behaviour and space use is based on older technology (e.g. Parker, Robbins & Hanley 1984; Parker 1988; Beier & McCullough 1990; Nelson 1995), and the data are therefore generally less extensive and often scale-specific. GPS-technology allows for a more holistic analysis of space use and movement patterns at different spatial and temporal scales, with the possibility of adding a wide range of covariates to determine the behavioural mechanisms behind the patterns observed.

Space use is affected by a wide range of factors, including environmental factors like habitat characteristics (quality and quantity of forage and cover; Mysterud & Ims 1998; Mysterud & Østbye 1999; Anderson *et al.* 2005), seasonal changes (Boyce *et al.* 2003; Börger *et al.* 2006), local weather (Parker, Robbins & Hanley 1984; Börger *et al.* 2006; Fieberg, Kuehn & DelGiudice 2008), and time of day (Armstrong, Euler & Racey 1983b; Beier & McCullough 1990). The effect of these factors may manifest themselves differently depending on the age and sex of the animal (Solberg *et al.* 2010; Ciuti *et al.* 2012), and also operate on widely different spatial and temporal scales (Johnson 1980; Senft *et al.* 1987; Wiens 1989; Börger *et al.* 2006). Knowledge about how factors such as climate and habitat selection function at different spatiotemporal scales is important for setting management rules for harvesting. On spatial scales, large scale movement patterns like seasonal migration and the establishment of home ranges are typically influenced by environmental factors operating on the landscape scale, while the animal's daily resting and foraging rhythms determine small scale movement patterns, like the use of different habitats within a home range (Morris 1987). The daily rhythm can also influence movement (e.g. habitat requirements) on short temporal scales, and the same is true for the difference in visibility between day and night. Large scale temporal variation in space use may arise due to seasonal variations in forage and climate (e.g. migration).

Due to the threat of global warming, research on climate change and the potential effects on animal populations have received increased attention (e.g. Parmesan 2006; Grosbois *et al.* 2008). In ungulates, weather can influence movement patterns such as migration, home range size and composition, and habitat requirements both directly and indirectly. Heat stress, cold stress and snow depth are typical factors affecting the animals directly through altered energy requirements (Barrett 1981; Parker, Robbins & Hanley 1984; Parker 1988; Arnold *et al.* 2004). Lower temperatures and increased precipitation have been shown to increase heat loss in ungulates (Barrett 1981; Parker 1988), and increased snow depth cause higher energy expenditures during movement, particularly when snow depths exceed critical limits such as breast height (Parker, Robbins & Hanley 1984). Heat stress may cause ungulates to alter their movement patterns when temperatures are above average (Dussault *et al.* 2004; van Beest, Van Moorter & Milner 2012), and this response is also likely to be correlated with increased insect loads. Movement responses to these direct climate effects are increased use of covered habitats (Dussault *et al.* 2004; Jenkins *et al.* 2007), decreased home range sizes (Beier & McCullough 1990; Börger *et al.* 2006) or shifting of the home range area (Ramanzin, Sturaro & Zanon 2007; Stien *et al.* 2010), and triggering of fall migration through cold spells and increased snow depth (Nelson 1995; Fieberg, Kuehn & DelGiudice 2008). Variations in temperature and precipitation may also influence animal behaviour indirectly, through plant growth (McNab 1963; Harestad & Bunnell 1979). Activity levels are affected by the availability and nutritional value of forage, i.e. earlier onset of plant growth is known to cause earlier spring migration in cervids (Albon & Langvatn 1992; Hebblewhite, Merrill & McDermid 2008; Bischof *et al.* 2012), and decreased nutritional value of forage in different habitats may cause increased movement and larger home range sizes to fulfil the animal's energetic needs (McNab 1963; Said & Servanty 2005).

Apart from food, ungulates may select closed habitats that offer cover from harsh weather conditions (e.g. Beier & McCullough 1990), predators or human hunters (e.g. Kunkel & Pletscher 2000). However, closed habitats usually hold lower qualities and quantities of forage than open habitats (Albon & Langvatn 1992). Available habitats thus hold a variety of costs and benefits for the animal, and they have to evaluate these when choosing where to move. The resulting choice of habitat is therefore a consequence of the trade-offs between these costs and benefits, and how they are perceived by the animal (Lima & Dill 1990). How the trade-offs are perceived and affect the animal can vary with weather, season, time of day and daily activity, and sex and age class (Beier & McCullough 1990; Mysterud & Østbye 1999; Manly *et al.* 2002; Ciuti *et al.* 2012). When activities are habitat-specific, such as the use of farmland for foraging and closed forests for cover, individuals may exhibit a functional response in habitat selection (Mysterud & Ims 1998). A functional response is present when the use of a specific habitat is neither proportional nor constant in relation to habitat availability, but rather that the relative use of this habitat changes between individuals due to variable availability. This behaviour has been documented in later studies (Boyce *et al.* 2003; Mauritzen *et al.* 2003; Osko *et al.* 2004; Gillies *et al.* 2006; Hebblewhite & Merrill 2008), but less attention has been paid to identifying the behavioural mechanisms behind this and how the functional response varies on spatial and temporal scales. As weather influences animal movement patterns and possibly the perceived trade-off between open and closed habitats, weather may also affect how much deer expose themselves to hunters – the harvesting vulnerability.

The main aim of this thesis is to identify the behavioural mechanisms determining space use and harvesting selection in red deer (*Cervus elaphus*) on different temporal and spatial scales, by looking at migration patterns, home range sizes and composition and within-home range habitat selection, and relating this to climate, habitat characteristics and hunter selection. As weather is an important factor influencing animal movement this area of research has achieved more focus, but available studies are still few and scale specific. The Norwegian red deer population offers a suitable study system, as they frequently switch between foraging in open agricultural areas and hiding in closed habitats offering less forage. From this system I have analysed detailed GPS-data on red deer movement from 123 individuals covering most of the distribution range in Norway, and harvest data with habitat of harvest, age, sex and date of culling from 11 municipalities. To be able to compare between different hunting cultures, and to look at long-term trends in trophy harvesting and hunter selection, harvest records covering the full distribution range of red deer in Hungary was used, including more than a century of data on the largest trophy sizes of males and 24 years of data with details on the total annual male harvest. More specifically, for each paper I aim to:

Paper I: Identify trade-offs and functional responses in habitat selection and the underlying behavioural mechanisms.

Paper II: Investigate how climate affects home range size at different temporal scales, disentangle direct and indirect effects of climate, and thus identify the behavioural mechanisms.

Paper III:	Investigate interaction effects between weather and space use, as well as sex and age class on harvesting vulnerability and hunter effort, and use this to identify the behavioural mechanisms causing potential differential harvesting vulnerability.
Paper IV:	Identify potential spatiotemporal variation in age-specific hunter selection, and to investigate if long-term trophy hunting causes phenotypic changes in a population of red deer.

STUDY SPECIES

Red deer in Norway

History, population size and distribution

The Norwegian red deer population represents the northernmost distribution of red deer in Europe (Koubek & Zima 1999; Sommer *et al.* 2008). The history of red deer in Norway can be traced back 8000 yr BP through the fossil record and through genetic data (Rosvold *et al.* 2012). At this time red deer were present southeast of Norway, and the population likely moved in from Sweden (Rosvold *et al.* 2012). The population size experienced a steady decrease over many centuries, reaching an all-time low of only a few hundred individuals found in isolated populations in the 19th century (Ahlén 1965). Probable contributions to this decline were heavy harvesting by human, predation pressure from wolves in particular, and habitat alterations caused by livestock occupying large areas of suitable red deer habitats for grazing. The population size stayed at low numbers isolated on the west coast of Norway, and did not experience a notable increase until the 1970s, after establishment of new management regulations (Statistics Norway 2012). During the last decades population increase has exploded, with red deer currently experiencing the historically largest population size and distribution range in Norway. Harvest numbers increased tenfold, surpassing moose harvest numbers in 2008 (Fig. 1; Statistics Norway 2012). Simultaneously, the distribution range expanded east-, south- and northwards from the core area on the west coast (Langvatn 1999; Statistics Norway 2012). The majority of the population is still found on the west coast, with more than 25% of red deer being harvested in the county of Sogn

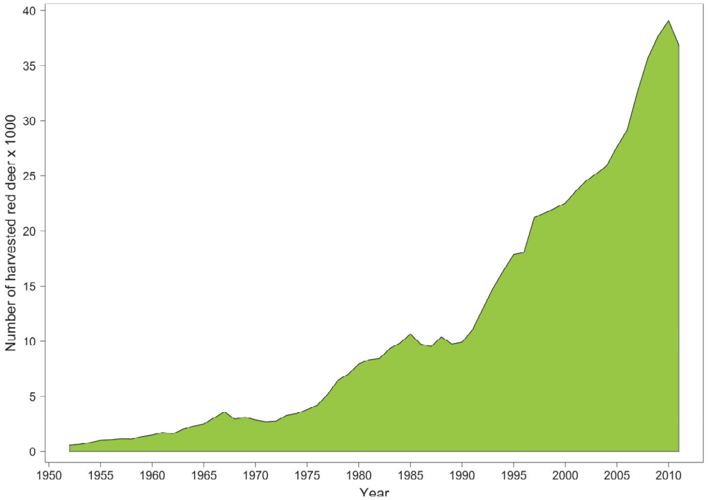

Fig. 1. Number of red deer harvested in Norway from 1952 to 2011(Statistics Norway 2012).

og Fjordane (Statistics Norway 2012). The population increase has been mediated to a large extent by strict management (Milner *et al.* 2006), but more favourable climatic conditions, in particular milder winters, have contributed considerable to both the increase and the range expansion (Mysterud *et al.* 2003).

General biology

The red deer is a highly sexually dimorphic species, with large difference in body weight (Mysterud *et al.* 2001b). Normal weight for adult males ranges from 180-240 kg, while adult females typically range from 100 to 115 kg, and body mass increase rapidly until 5 and 4 years old for males and females respectively (Langvatn & Albon 1986). Northern cervids typically migrate between distinct summer and winter ranges in spring and fall, and the red deer is no exception (Albon & Langvatn 1992). However, Norwegian red deer are partial migrators, meaning that in the population some individuals migrate, while others are stationary or adopt yet other strategies (Bischof *et al.* 2012). For migrators, summer ranges are located at higher elevation and/or further inland, where younger, more nutritious plants are available for longer time periods (Albon & Langvatn 1992; Pettorelli *et al.* 2005). Due to the increased amount of snow present inland and at higher elevations in winter, the winter range is typically situated at lower elevations and/or closer to the coast, and often with greater access to farmland (paper I, paper III, Nelson 1995; Fieberg, Kuehn & DelGiudice 2008). Spring migration usually take place in April-May, but variation in individual red deer is reported from late March to mid-July (Bischof *et al.* 2012). Return to the winter range in fall is commonly conducted in September-November, but here to variation is large (from end of July to December; unpubl. data). The red deer prefer areas where forage- and cover habitats such as deciduous forests, pastures, and also planted Norway spruce (*Picea abies*; important cover habitat), can be found within relatively close range (paper I, Mysterud *et al.* 2002). Classified as mixed feeders (Hofmann 1985), popular red deer forage during summer include graminoids, herbs and shrubs (Albon & Langvatn 1992). The winter diet is considerably lower in protein and high in fibre due to plant senescence, and is mainly composed of bilberry (*Vaccinium myrtillus*) as well as other shrubs and browse (Ahlén 1965). Pastures are utilized to a large extent when forage is scarce in other habitats (paper I).

Males mature around 1-3 years of age, and females around 1.5-2.5 years, but age at first reproduction is highly dependent on body weight for females (Langvatn *et al.* 2004), and males rarely invest energy into the rut until they reach 3-4 years (Yoccoz *et al.* 2002). Mating takes place in October (median ovulation date October 15th; Langvatn *et al.* 2004), and there is a distinct rutting period where males defend harems of females or land occupied by females from other males (Clutton-Brock, Guinness & Albon 1982). In Norway these harems are typically small compared to e.g. Scotland, probably due to the rugged terrain and habitat characteristics complicating the defence of females. A single calf is born in June (median calving date June 16th; Loe *et al.* 2005). The calf remains hidden in dense vegetation during the first days after birth, until it gains enough strength and body weight to follow the mother. Sociality is highly dependent on season (Bonenfant *et al.* 2004), and outside the rutting season, young males may aggregate in smaller bachelor groups, while prime-aged males tend to lead a more solitary lifestyle. Females stay in matrilineal groups consisting mainly of related females and their offspring.

The oldest age reported for males is 22 years, and 26 for females (Mysterud *et al.* 2001b). However, reaching such an old age is a rarity, as the harvesting effort is very high. Harvesting is the main cause of death in Norwegian red deer, and more than 80% die from being shot during the hunting season (September 10th - November 15th; Langvatn & Loison 1999). This means that harvesting basically determines survival. Hunting pressure is particularly high for young individuals like calves and yearlings, and males up to 3 years (Veiberg, Nilsen & Ueno 2010), and the probability of being harvested is also higher for adult males than for adult females (Langvatn & Loison 1999). Consequently, a male has 52% chance of surviving from 1.5 to 2.5 years, and 55% of surviving the next year and reach age 3.5 years. For females, survival is considerably higher (81% and 82% chance of surviving from 1.5 to 2.5 years and 2.5 to 3.5 years respectively; Langvatn & Loison 1999). At the present, predators are scarce in Norway, and particularly in the core area on the west coast. Thus, few animals are killed by predators. Other causes of death are vehicle collisions and severe winter conditions. The latter has a large effect on calves (Loison, Langvatn & Solberg 1999).

Red deer in Hungary – comparison with the Norwegian red deer

The population size in Hungary have experienced the same dramatic increase as in Norway, with 3800 red deer harvested in 1960 and 36679 in 2005 (Csányi & Lehoczki 2010). However, the overall estimated population size is lower (~80000 in Hungary vs. ~130000 in Norway; Apollonio, Andersen & Putman 2010). Similar aspects as in Norway have mediated the population growth through density increase and range expansion, and in addition newly afforested areas have been established and contributed heavily (Csányi & Lehoczki 2010).

The Hungarian management regime differs from the Norwegian, as, in addition to keeping population numbers at an optimum where damage is controlled and population size is sufficient for maintaining genetic diversity (Csanyi 1991), they also aim to maintain a high quality and quantity of trophy stags through selective harvesting and compensatory culling (Csik 1902; Széchenyi 1948; Mysterud & Bischof 2010). Red deer stags in Hungary have considerably larger trophies (antler size) than the Norwegian red deer, also holding several world records from the International Council for Game and Wildlife Conservation (CIC; Fig. 4; paper IV; CIC 2010; Csányi & Lehoczki 2010). The Norwegian and Hungarian red deer were isolated in separate refugia during the last glaciation (Skog *et al.* 2009), indicating that the variation in antler size between the two populations probably has a genetic component, but due to the long trophy hunting tradition in Hungary going more than a century back in time, with hunting tourism from foreign hunters, management is likely to have contributed to the increased trophy sizes in Hungarian red deer. It should be noted that red deer surviving to old ages experience senescence where body weight decreases with increasing age (Mysterud *et al.* 2001b), and, important for the trophy hunting tradition in Hungary, antler size also decreases (Fig. 2). Foreign hunters prefer the largest prime-aged stags (7-12 years old; paper IV), and the age-specific antler size decreases after age 12 (Fig. 2). Also, local hunters shoot a much larger proportion of young stags, and stags with smaller age-specific antler size (Fig. 2; paper IV).

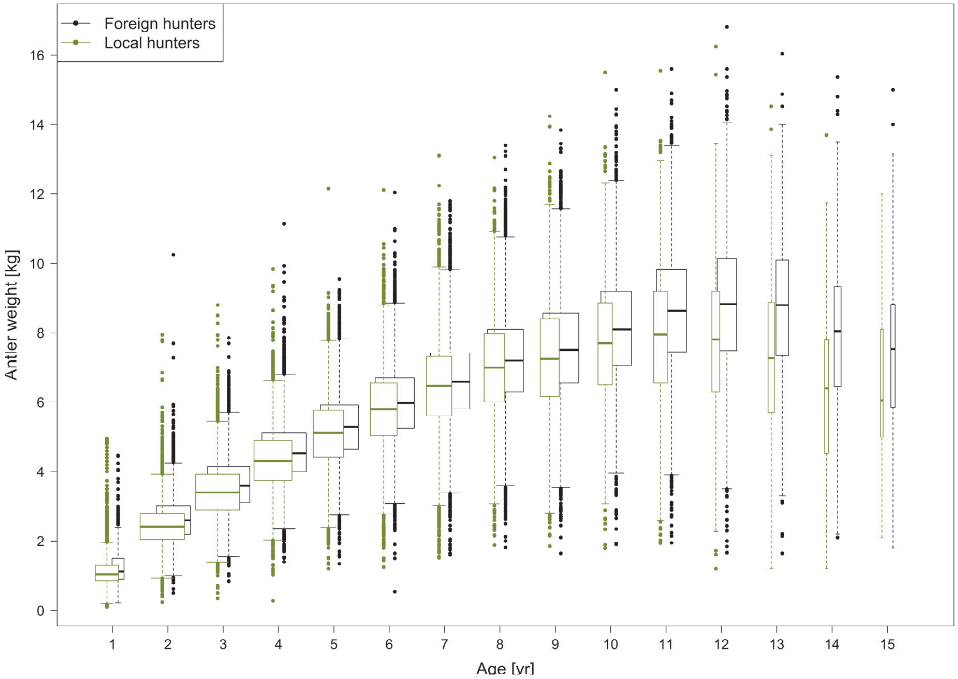

Fig. 2. The age-specific antler sizes in kg of red deer stags harvested by foreign (black) and local (green) hunters in Hungary from 1973-2008. The width of the boxes represents the relative number of individuals harvested by the hunter types and in each age class.

STUDY AREAS

Norway

The Norwegian study area covers the core distribution area for red deer on the west coast of Norway (counties Hordaland, Sogn og Fjordane, Møre og Romsdal and Sør-Trøndelag), as well as the inland county Buskerud (Fig. 3). In this region both vegetation and climate follow a characteristic coast-inland gradient. Precipitation and temperature decline from coast to inland and from south to north, while snow depth and the duration of snow cover increase (Langvatn *et al.* 1996). On the west coast of Southern Norway (counties Hordaland, Sogn og Fjordane, Møre og Romsdal and Sør-Trøndelag), the vegetation is mostly in the boreonemoral zone, except for a small area around Hardangerfjorden in Hordland, which is in the nemoral zone, and an area around Trondheimsfjorden in Sør-Trøndelag characterized as southern boreal. The inland region (Buskerud) has vegetation characterized as northern boreal (Abrahamsen *et al.* 1977). Forests from Hordaland to Møre and Romsdal are mostly deciduous dominated by birch (*Betula* sp.) and alder (*Alnus incana*), as well as pine forests (Scots pine, *Pinus sylvestris*). Norway spruce has been planted on a large scale, and stands are dense with little ground vegetation. Farmland in this area is dominated by timothy (*Phleum pratense*) for grass production. In Sør-Trøndelag towards Trondheimsfjorden, forests consist mainly of Scots pine and birch, and north of Trondheimsfjorden Norway spruce is the dominating species. Inland forests typically consist of coniferous species such as Norway spruce and Scots pine.

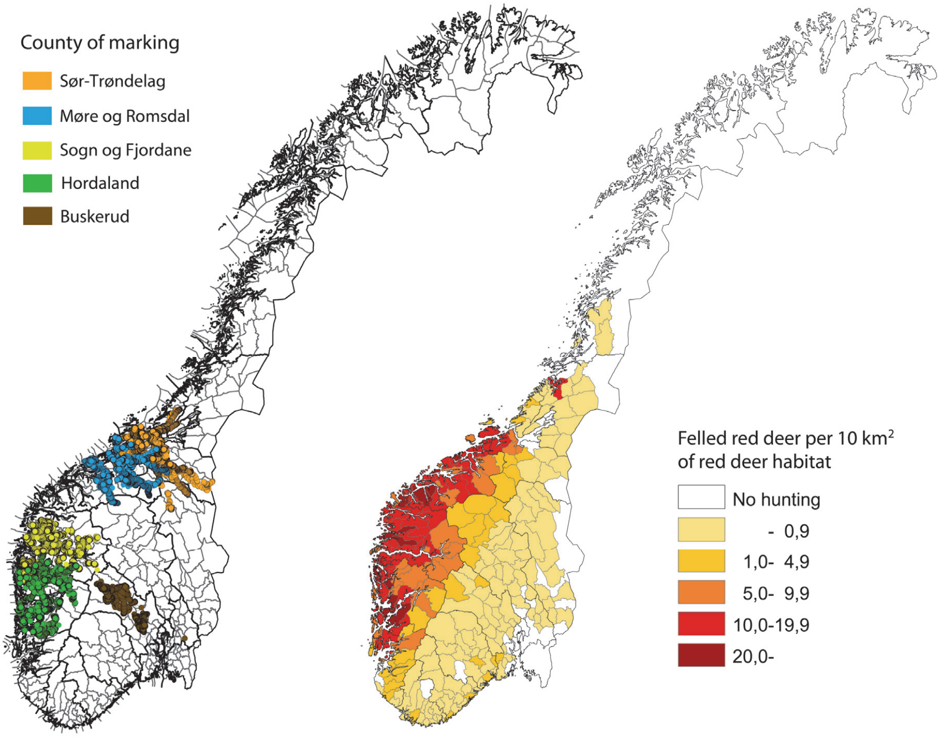

Fig. 3. Map of Norway showing the study areas with our data on GPS-collared red deer (left) and the distribution of Norwegian red deer at the municipality level based on harvest statistics from 2011 (right; harvest map from Statistics Norway, 2012). Colours on the left map represent the different counties where the red deer are marked, and dots are individual GPS positions.

Hungary

The study area in Hungary covers the full distribution range of the Hungarian red deer. Red deer are mainly distributed in Western and Northern Hungary, with the core area in the counties Baranya, Sornogy and Zala in the southwest (Fig. 4). In Western Hungary topography is characterized by rolling, forested hills, low mountains, valleys and plains, and a few mountainous regions are also present. The north is dominated by forested mountains and hills. In general, Hungarian soil is fertile with a rich flora. The climate is mild and continental with influences from the Mediterranean and the Atlantic, conditions which together are highly suitable for agriculture. Consequently, agricultural fields have dominated the landscape since the 19th century (Csányi 1997). Heavy measures was taken to increase forestry production after 1945 (Csányi 1994), and today 19% of the country is covered by forests. Most forested areas are found in the mountains in the north, but some forest is also present in the low mountains and hills of Western Hungary. Forest vegetation is characterized by temperate broadleaved deciduous forests dominated by oak (*Querqus* sp.), beech (*Fagus* sp.) and willow (*Sailix* sp.). A few areas with coniferous forests (mostly fir; *Abies* sp.) also exist. Of the forested regions in Hungary today, ≥70% originate from forest plantations (Csányi 1997).

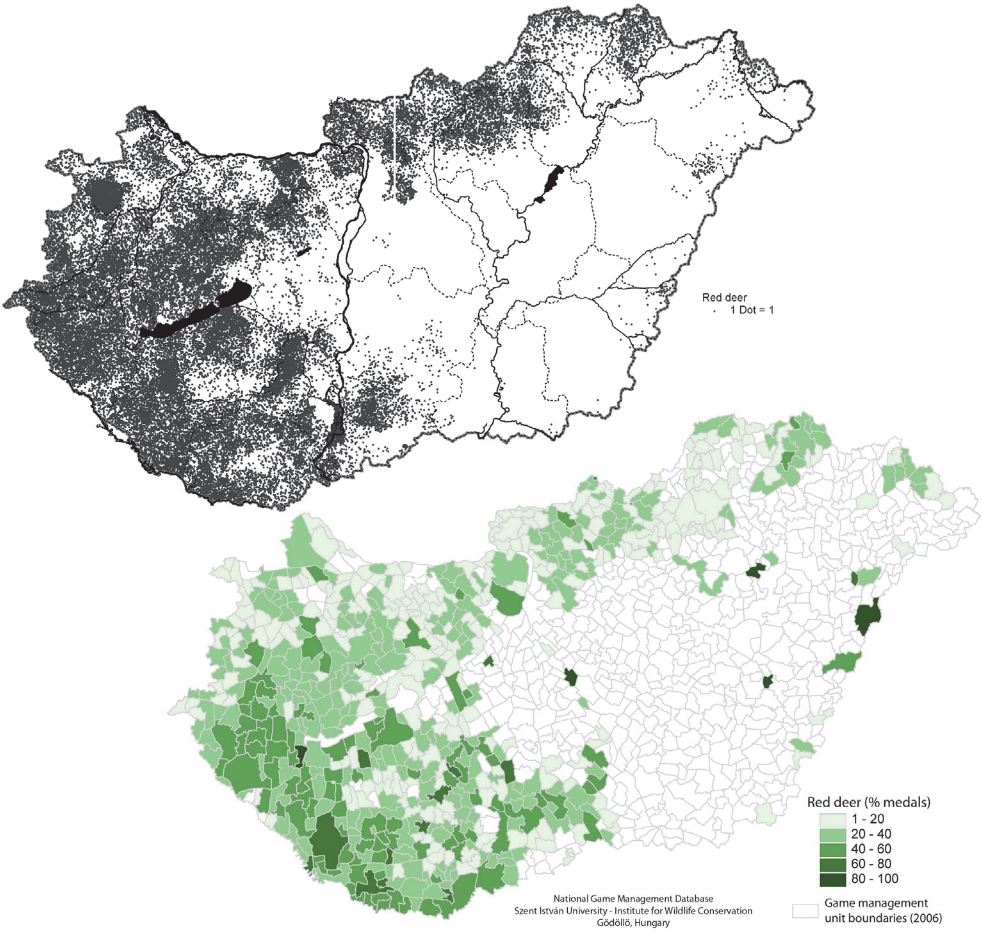

Fig. 4. Map showing the distribution of harvested red deer in Hungary (top) for the hunting season 2011/2012. 1 dot on the map represents one harvested red deer. The lower map shows the distribution of trophy stags, with different shades of green representing the percentage of stags with trophy size qualifying for medals out of all stags harvested between the 1997/1998 and the 2007/2008 hunting season (maps provided by the National Game Management Database, Szent István University, Institute for Wildlife Conservation, Gödöllö, Hungary).

MATERIALS AND METHODS

Movement patterns of marked individuals

Movement data in paper I, II and III are from GPS-collared red deer caught by darting on winter feeding grounds in Norway, using methods approved by the Norwegian national ethical board for science. The GPS-collars came from Televilt/Followit, Stockholm, Sweden and Vectronic, Berlin, Germany. The data in paper I and II come from a subset of the current available GPS-data on red deer and covers only the county of Sogn og Fjordane, while data in paper III cover all counties listed under "Study area" (Norway; Fig. 3). In addition, individuals with VHF-collars (Televilt/Followit) were used in paper I, caught by the same method as the GPS-collared individuals. These data come from Sogn og Fjordane. See the individual papers for more details on logging schedules, observation numbers, general screening of data and more.

GPS-telemetry used in animal tracking can generate huge amounts of valuable data covering long time periods. However, working with GPS- (and VHF-) technology forces the researcher to consider possible sources of bias that can influence the results of the analyses, as GPS-technology frequently contain errors (Frair *et al.* 2004; D'Eon & Delparte 2005; Bjørneraas *et al.* 2010). Common sources of errors are variable success rates (missed locations) and location errors of successful GPS-locations (Frair *et al.* 2004; Lewis *et al.* 2007). Both sources are often influenced by environmental conditions (D'Eon & Delparte 2005; Graves & Waller 2006) and animal behaviour (Moen *et al.* 1996; Bjørneraas *et al.* 2010) in addition to potential technological problems. I will address these issues in more detail below.

Success rate of GPS-collars

The largest source of error is probably variations in the success rate of getting a location (fix rate) and consequent missing data (D'Eon 2003; Frair *et al.* 2004). The severity of the consequences of a fix rate lower than 100% varies depending on the scale you wish to analyse data. E.g. for home range analyses, a lower fix rate can be tolerated if the missing locations are spread out approximately equal over the period for which you wish to calculate the home range, and if there are no border areas in the home range with very low probability for a GPS fix. When analysing habitat selection, a fix rate closer to 100% is more important as selection estimates can be biased if a certain habitat type generates a lower fix rate than others (D'Eon

& Delparte 2005). This is a very plausible scenario with environmental characteristics influencing the fix rate (Graves & Waller 2006), and it's a concern of importance when comparing open habitats (e.g. farmland) with covered habitats (e.g. forests) as canopy cover can have a negative effect on the fix rate (D'Eon *et al.* 2002).

Habitat selection at the within-home range scale was investigated using GPS-collars in paper I. The success rate of the collars worn by the red deer averaged 91% (range 77-98%), and the problem of missing locations should therefore be addressed. To assure that a variable fix rate did not bias our results, a method called iterative simulation was used prior to analyses (Frair *et al.* 2004). In short, this method fills in the missing locations (all failed locations and locations deleted as outliers) between the last and next known location, based on a map containing probabilities of acquiring a fix for each pixel (see Appendix A of paper I for details). The probability map was constructed by conducting a field study in the red deer study area where stationary GPS-collars (Televilt/Followit) were placed in every combination of habitat (open = pasture; closed = forest), slope (flat <10º, moderate = 10-20º, steep >20º) and aspect (north = 315-45º, south = 135-225º). In addition, several characteristics of the trial site were measured in the field including percentage open canopy, tree density, tree height, tree diameter and horizontal view, and terrain variables including slope, aspect and altitude at the test site, and percentage visible sky were derived from Geographic Information System (GIS). We compared results using both the corrected and the uncorrected data set, and found a high degree of qualitative consistency between them, but with a generally lower odds ratio of selection in the uncorrected data set. From this, we can conclude that the fix rate obtained in this study is sufficient for analyses of habitat selection at the within-home range scale.

In paper II home range sizes were calculated on four different temporal scales, based on GPS-data. To ensure sufficient coverage in time in case of variable fix rates, and that locations were spread out over the entire time period, we only estimated home ranges for periods with at least 95% coverage of the given time interval, and at least 16 relocations.

GPS-data was used to identify fall migration dates in paper III, and the fit of the estimated fall migration dates to the actual movement data was checked by visual inspection (Bischof *et al.* 2012). As a continuous stream of locations is needed to identify migration properly, variable fix rates in or around the fall migration could not be tolerated, and individuals with longer periods of missing locations around the migration period were excluded.

Location accuracy

The location accuracy of the GPS-collars used in the study was determined from the field study with stationary GPS-collars mentioned above. The location error was estimated by calculating the linear distance between the assumed true position of the collars (the 24 hour mean location) and the recorded GPS positions in the collars. The median location error was 12 m, which is comparable to earlier reports (D'Eon & Delparte 2005). Knowledge about the magnitude of the location error is more important for fine scale studies of movement such as habitat selection, than for more large scale movement (home range scale, migration patterns), at least when the location error is as small as in this study. I intended to use the data for habitat selection analyses and thus link the data to habitat characteristics using GIS-technology. For such analyses the resolution of the pixels in the habitat maps should be larger than the GPS location error. The maps used had a resolution of 50x50 m, which is larger than the estimated median location error of 12 m, and the habitat selection analyses should therefore not be biased due to GPS location errors.

VHF-collars and accuracy

To locate the position of a VHF-collared deer, tracking was done by car or by foot, and at least three bearings were taken for each individual. With three or more bearings, the confidence area for a location can be estimated (White & Garrott 1990). However, without approaching and visually observing the actual location of the VHF-collared individuals, the positions will naturally be less accurate than positions from GPS-collared individuals, where several satellites are used for accuracy (number depending on the geographical position of the device and on local topography; D'Eon & Delparte 2005). I therefore used the program LOAS 4.0b (Ecological Software Solutions, Florida, USA) to perform a visual inspection of all bearings, and estimate the individual locations and the associated error ellipses (confidence area). If these ellipses are large, the data may not be suitable for detailed and small-scale analyses such as habitat selection, as the real location could be in a neighbouring habitat type. To investigate this, one can measure the size of habitat patches within the individual animals' home ranges, and compare these to the size of the error ellipses. In the localization of the VHF-collared red deer the error ellipses were generally small (mean 10.65 hectares (ha) [95% confidence interval (CI) 8.70-12.60 ha] and median 1.85 ha [range 0.00-675.66 ha]; see Appendix B of paper I, Fig. B1) and comparable to the size of the habitat patches within the individual 100% seasonal minimum convex polygon home range (mean 4.41 ha [95% CI 3.62-5.20 ha] and median 0.44 ha [range 0.00-436.00 ha]).

Harvest data and hunter selection

As data from long-term monitoring of individuals is rare and hard to obtain from large, harvested populations, harvest records are frequently used to study both life history traits (e.g. Langvatn *et al.* 1996; Mysterud *et al.* 2001a; Mysterud *et al.* 2002, see chapter on red deer biology for more examples) and patterns of harvesting selection (Martinez *et al.* 2005; Mysterud, Tryjanowski & Panek 2006; Torres-Porras, Carranza & Perez-Gonzalez 2009). The harvest data in paper III and IV and data on long-term trends in trophy size in paper IV stem from culled red deer in Norway (paper III) and Hungary (paper IV). However, such data should be interpreted with caution, as they may represent a biased sample of the population due to hunters being selective for specific traits (Solberg *et al.* 2000), or managers and quotas making individuals of a certain sex or age class more prone to being culled (Ericsson & Wallin 2001). When using harvest records to investigate hunter selection, this must be taken into account.

Use of harvest data to measure hunter selection

When measuring hunter selection in a harvested population, it’s central to know the underlying population structure and thus what the hunters have the opportunity to select from. However, as mentioned above this kind of long-term monitoring data is expensive and time-consuming to obtain, and rarely exist for harvested populations (review in Mysterud 2011). Without knowledge about the actual population structure, patterns of harvesting selection in ungulate populations can be studied by comparing categories of hunters (e.g. local hunters vs. foreign trophy hunters; Mysterud, Tryjanowski & Panek 2006) or hunter methods (Martinez *et al.* 2005; Torres-Porras, Carranza & Perez-Gonzalez 2009). All hunters, regardless of method or category, hunt the same population for a given year, but are expected to differ in how effective they are and in their motivation for hunting. Thus, any differences in the average trait size between categories of hunters or method used is expected to reflect a difference in selection, at least for a given year. Note that between-year variation may be less comparable, as the preferences of the different categories may change due to e.g. variable economy, at least when comparing over longer time scales. To measure hunter selection in the

Hungarian red deer harvest, I compare the age-specific antler size of deer harvested by local hunters with the size of deer harvested by foreign trophy stalkers. These groups are expected to have quite different motivations for hunting, with foreign trophy stalkers often paying a lot of money to hunt large individuals, while local hunters are mainly responsible for culling of young and small males.

Potential bias in long-term trophy size data

The data on long-term development in trophy size used in paper IV stem from trophy exhibition records. In these exhibitions only the very largest trophies are shown. These data therefore represent a biased sample from the population, only including the upper end of the size scale, and any temporal trends in trophy size may be underestimated. Pelletier *et al.* (2012) investigated this problem by comparing horn size of bighorn sheep from harvest records with those recorded by proper monitoring during a period of known decline. Although the magnitude differed, the decline in horn size was identified by both data sets, showing that harvest data can be useful for identifying long-term trends in trait sizes.

RESULTS AND DISCUSSION

Habitat selection, trade-offs and temporal scales (paper I)

The use of open habitats with higher plant quantity and quality for foraging and closed habitats with more canopy cover for resting and rumination is well-known in temperate ungulates, such as red deer (Staines 1976), roe deer (*Capreolus capreolus*; Mysterud & Østbye 1995) and white-tailed deer (*Odocoileus virginianus*; Armstrong, Euler & Racey 1983b; Armstrong, Euler & Racey 1983a). The trade-off between the use of open and covered habitats commonly relates to the quantity and quality of forage available (lower in covered habitats due to shading of plants; Mysterud *et al.* 1999). The use of open and covered habitats is also related to time of day, with higher use of covered habitats during daytime and open habitats during night-time (Armstrong, Euler & Racey 1983a; Beier & McCullough 1990). When the use of covered and open habitats varies with activity level and time of day, the behaviour is commonly interpreted as a response to predator threats (Lima & Dill 1990; Mysterud & Østbye 1999) and/or canopy cover offering thermoregulatory benefits due to unfavourable climate (review in Mysterud & Østbye 1999) and reduced energy expenditure of movement due to shallower snow depths (Parker, Robbins & Hanley 1984).

This trade-off is well known across a diverse range of species (Lima & Bednekoff 1999; Reckardt & Kerth 2007), but few studies have quantified the strength of these trade-offs by separating the data set by time of day or state of activity. This change in habitat selection between time of day and state of activity is likely to give rise to a functional response, where the selection of a given habitat is dependent on the availability of that habitat type (Mysterud & Ims 1998). A few studies have measured a functional response in habitat selection (e.g. Boyce *et al.* 2003; Gillies *et al.* 2006; Hebblewhite & Merrill 2008); however none of these have identified the underlying behavioural mechanisms by which this arises at the individual level. To identify these mechanisms I test three distinct hypotheses. Hypothesis H_1 states that temporal scale is important for habitat selection, and predicts a higher selection of open habitats during darkness than daylight. Habitat selection was analysed in two different populations in Sogn og Fjordane, one equipped with GPS-collars (Sunnfjord) and one with VHF-collars (Nordfjord). As only the VHF-collars contained activity switches, we had to assume that activity levels for all individuals were higher during darkness and twilight, a relationship that has been shown in cervids in many earlier studies (e.g. Georgii 1981; Beier

& McCullough 1990; Carranza *et al.* 1991; Ager *et al.* 2003). The activity levels of the VHF-collared red deer in our study area supported this assumption (see paper I, Fig. 3). The overall selection pattern was similar in both study areas, and, supporting H_1, selection for open habitats (pastures) was highest during darkness and lower during daylight, while selection for covered habitats (forest of high productivity) was higher during daylight (see paper I, Fig. 2). Habitat selection also differed somewhat between seasons, with higher selection of pastures in spring and autumn than in winter and summer.

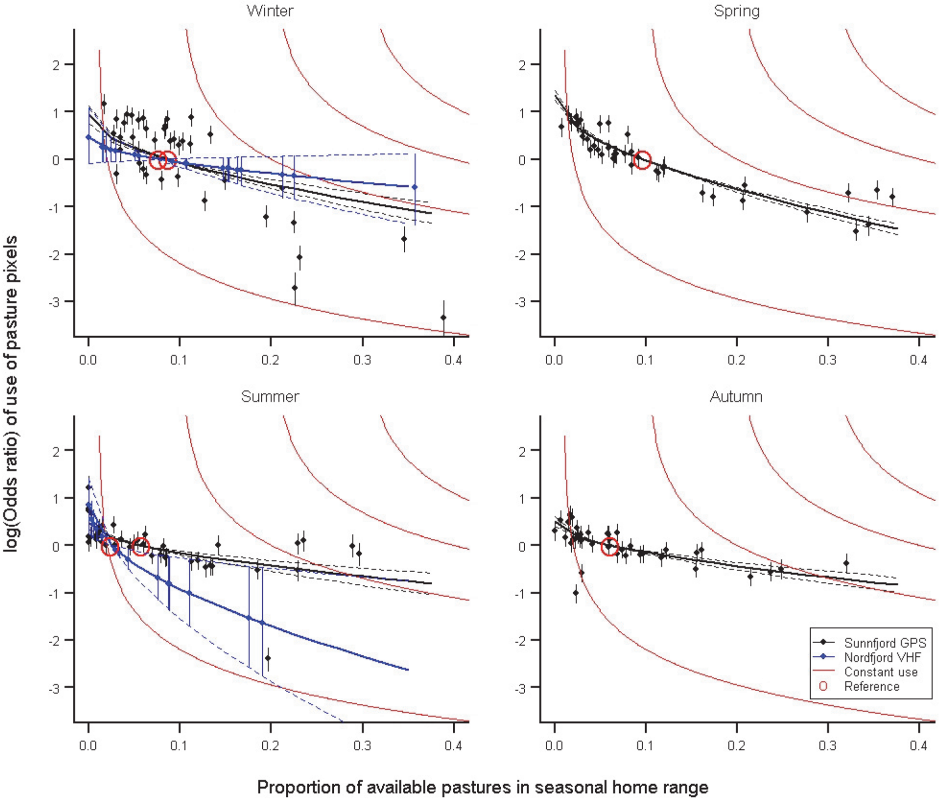

Fig. 5. Functional response in the selection of pastures of red deer in Sunnfjord (GPS-collared; black) and Nordfjord (VHF-collared; blue). The log odds ratios of the use of pasture pixels are calculated relative to the average available pastures in the seasonal home range (red circles) and provide a measure of selection. The points are individual red deer; error bars and dashed lines represent 95% highest posterior density intervals. Red lines illustrate constant use of pastures, while a hypothetical horizontal line (slope=0) would indicate proportional use.

The identified change in habitat selection between day and night and activity level means that activities are habitat- and scale-specific, which will give rise to a functional response (Mysterud & Ims 1998). Hypothesis H_2 therefore states that use of a given habitat is expected to be neither proportional nor constant, but somewhere in between, e.g. a functional response in habitat selection. From this I predict that selection of pastures should increase (i.e. not proportional use), but the time spent on pastures should be reduced (i.e. not constant time use), with lowered availability. This prediction was supported in both regions, as the selection of pastures declined with increasing availability across all seasons (Fig. 5). Red deer spent more time on pastures with increasing availability, but not proportionally more, and the selection was not constant, but somewhere in between these two extremes (Fig. 5).

Finally, in a seasonal environment the distribution of forage and cover is expected to vary largely over habitats throughout the year. This is likely to affect the relative amount of resources in the different habitat types, and thus create seasonal variations in the strength of the functional response, a hypothesis (H_3) which has not been addressed in earlier studies. H_3 predicts a more pronounced functional response during seasons when the difference in quantity and quality of forage in open and closed habitat is larger. The functional response showed seasonal variation, but the pattern differed between regions (Fig. 5). In Sunnfjord, the response was strongest during spring, and supporting H_3 it was weakest during summer. The Nordfjord populations exhibited the strongest response in summer and the weakest in winter. This difference may arise due to an interaction between seasonality and landscape architecture, as the habitat composition within the individual home ranges in the two regions differed (15.5% more forest of high productivity and 12% less marshland and mountains in Nordfjord).

Home range size variation at different spatiotemporal scales (paper II)

Within species, home range size varies both on the spatial and temporal scale. Spatially, home range size is closely linked to habitat productivity and energetic requirements (Ford 1983; Tufto, Andersen & Linnell 1996) with increasing productivity leading to smaller home ranges (Kie *et al.* 2002; Anderson *et al.* 2005; Börger *et al.* 2006). Temporally, the size is known to vary with seasons (Georgii 1980; Georgii & Schroder 1983; Börger *et al.* 2006). Seasonal variations in climate are predictable and the effect on home range size is well known, but climate may also affect home range size on shorter time scales through more unpredictable changes causing thermal stress and more sudden variations in forage availability and energy requirements (Parker, Robbins & Hanley 1984; Van Soest 1994; Börger *et al.* 2006). Currently, knowledge about how local climate and other environmental factors (e.g. habitat composition) affect intraspecific home range size on different temporal scales is limited (Börger *et al.* 2006; Said *et al.* 2009).

As different biological processes may operate on particular temporal or spatial scales (Senft *et al.* 1987; Wiens 1989; Levin 1992), factors determining red deer home range size on four different scales (monthly, weekly, two weeks (biweekly) and daily) were explored. The environmental factors used were weather (temperature, precipitation and snow depth; all fitted as residuals from a regression against daylight to remove the seasonal patterns), day length and dominant habitat type within the home range. I found that, depending on the temporal scale, the effect of local climate on home range size differed. When comparing effects of weather on patterns of home range size on long and short temporal scales, it is possible to infer whether the effect of local climate on animal movement and activity is likely to be direct or indirect. Direct effects of weather (except snow depth) are likely to operate more strongly on short temporal scales (daily-weekly) influencing red deer home range size directly through altered activity (Parker 1988; Beier & McCullough 1990), while indirect effects of local climate operating through plant growth should be stronger on longer temporal scales (biweekly-monthly). Results were consistent with both indirect and direct effects of climate, and the relative strength of these could also be estimated.

As predicted, home range size increased when temperatures were higher than normal during winter and decreased with higher temperatures during summer (see paper II, Fig. 1). Direct effects of temperature such as heat stress during summer and cold stress during winter have earlier been found to reduce animal activity, and hence home range size (Beier & McCullough 1990). The effect of precipitation was more variable depending on season and temporal scale (see paper II, Fig.2). On the biweekly and monthly scale I found a positive relationship between precipitation and home range size throughout the year, while on shorter temporal scales (daily-weekly) the effect of precipitation was dependent on season with home range size changing in the same manner as for temperature (positive relationship in winter and negative in summer). The negative relationship between precipitation and home range size found on short temporal scales in summer was therefore consistent with decreased activity as an energy conservation strategy during heavy precipitation, as earlier found in black-tailed deer (*Odocoileus hemionus columbianus*; Parker 1988). I analysed the effect of snow depth separately, and as expected, home range size decreased when snow depth was larger than normal, and the effect was strongest on large temporal scales (see paper II, Fig. 3). Increased snow depth causes higher energetic expenditures through movement in snow (Parker, Robbins & Hanley 1984), and thus also a decrease in home range size, but contrary to the other local climate variables, snow depth persists for longer periods and should therefore have a stronger influence on home range size at longer than shorter temporal scales.

I found a correlation between temperature during summer, which can be used as a crude estimate of plant productivity, and home range size also on long temporal scales (see paper II Fig. 1). This is indicative of indirect effects of local climate on home range size, as plant growth is likely to have a larger influence on home range size on the longer temporal scales. Plant quality and quantity is likely to influence movement patterns and activity, and thus also home range size through the available forage's ability to fulfil the energetic needs of the animal (paper I; McNab 1963; Harestad & Bunnell 1979). Also, day length can be used as a crude estimate of available energy and forage within the home range (Kjellander *et al.* 2004; Anderson *et al.* 2005; Ramanzin, Sturaro & Zanon 2007), and can therefore also be used as measure of indirect effects. The effect of day length was negatively correlated with home range size, but only on the monthly and daily scale (sees paper II, Supporting Information, Fig. S3). The lack of a more consistent effect of day length may be due to a relationship between the forage quantity and quality and higher energy demands of lactating females during summer (Hanwell & Peaker 1977; Clutton-Brock *et al.* 1982). Further, as home range size is closely related to energetic requirements (McNab 1963; Harestad & Bunnell 1979), I investigated the effect of habitat composition on home range size. As expected, home ranges dominated by forage-poor habitat types were larger than home ranges dominated by habitat types rich in forage or habitats where a mixture of forage and cover could be found (see paper II, Fig. 4). The effect was apparent on all temporal scales except on the monthly scale, further supporting that the main determinants of home range size is habitat differences related to variation in forage quantity and quality.

To determine whether the direct or the indirect effects of local climate were more important in determining home range size, I compared the strength of the slope estimates across all scales. The effect of local climate were strongest on the longest temporal scale (monthly), which indicates that the indirect effects operating through vegetation development

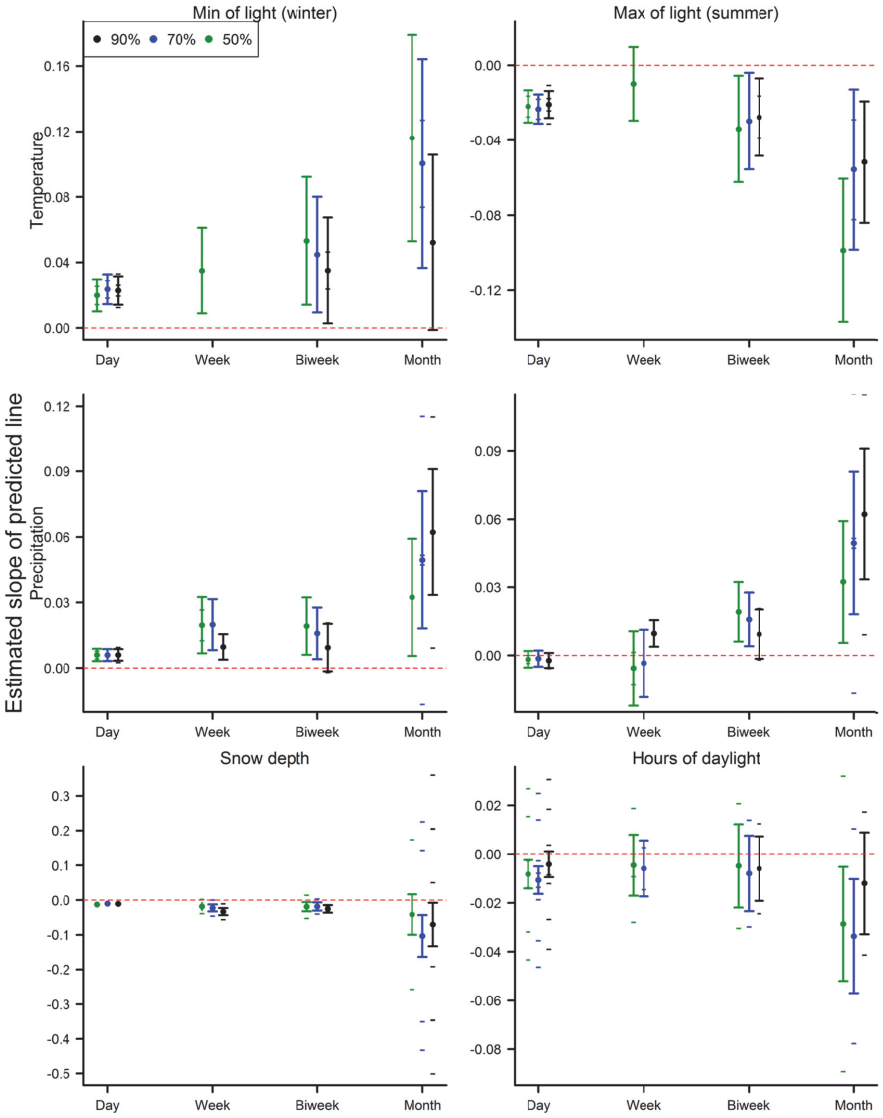

Fig. 6. Plots of estimated slopes and 95% confidence limits of the predicted lines of temperature and precipitation (from paper II, Figs 1 and 2) and snow depth and hours of daylight (from paper II Figs 3 and S3 [Supporting Information]) for each temporal scale (x-axis) and for the 90, 70 and 50% kernel estimates (shown in black, blue and green respectively). The dotted line illustrates slope = 0, meaning the variable exhibits no significant effect on home range size. Predictions are done for reference values given in the figures shown in paper II, and horizontal bars show how the slope changes if the reference values of interacting covariates are altered ± 1 SD away from the mean.

and abundance were stronger than the direct climatic effects (Fig. 6). However, direct and indirect effects of climate are clearly not mutually exclusive at any temporal scale, but it’s likely that the relative importance may vary across scales. The use of an established multi-scale approach (Börger *et al.* 2006) in a novel way made it possible to distinguish the relative importance of direct and indirect effects of local climate on animal behaviour and subsequent movement patterns and activity.

Climate, habitat and selective harvesting (paper III)

The effects of climate and habitat characteristics on red deer behaviour and movement patterns found in paper I and II are expected to influence how much the animals expose themselves to hunters, i.e. the harvesting vulnerability. In addition, prevailing weather may also influence the behaviour of the hunter, and subsequently the hunter effort. Environmental features such as local climate and habitat characteristics are known to affect predator-prey relationships (Post *et al.* 1999; Kunkel & Pletscher 2000; Lebel *et al.* 2012), and in a human harvesting setting the hunter can be viewed as predator and the targeted animal as prey (Nugent & Choquenot 2004). A large number of studies have investigated how selective harvesting affects deer populations (e.g. Solberg *et al.* 1999; Milner, Nilsen & Andreassen 2007; Mysterud, Yoccoz & Langvatn 2009; Servanty *et al.* 2009), but how weather may affect harvesting indirectly through animal and/or hunter behaviour is not well known. In addition, individuals of different age and sex classes are expected to behave differently, and how this affects harvesting risk is uncertain (Bunnefeld *et al.* 2009; Solberg *et al.* 2010; Ciuti *et al.* 2012).

Paper I showed that climate affects the use of open and closed habitats, and in this study I wanted to quantify in more detail how prevailing weather influences the probability of being harvested in open, forage-rich habitats (farmland), as well as the effect of weather on total harvest numbers and on hunter effort. Weather is also known to affect the timing of fall migration in northern migratory cervids (Nelson 1995; Fieberg, Kuehn & DelGiudice 2008). In Norway the fall migration period for red deer coincides with the harvesting season, and indirect effects of weather on harvest processes are expected. Decreased temperature (days with <0ºC) showed a clear relationship with the timing of fall migration, and increased snow depths (days with >10 cm) showed a somewhat weaker relationship (see paper III, Fig. 1).

This relationship was still apparent when accounting for potential seasonal trends (see paper III, Supporting information, Figs S1-S2). As snow depth and temperature were identified as triggers of fall migration, I also expected higher harvest numbers in the winter range after first snow fall, but found no evidence for this. Higher use of covered habitats during increased snow depths (Parker, Robbins & Hanley 1984) could make them less available for hunters, and remove the effect of first snow fall. In general, the relationship between fall weather conditions, habitat characteristics and harvesting risk was highly variable through the season (see paper III, e.g. Fig. 5). For certain periods we found patterns consistent with the expected use of forage and cover in relation to temperature and precipitation (Mysterud & Østbye 1999), i.e. with low temperatures yielding low harvest numbers and lower hunter effort late in the hunting season (Curtis 1971), but not consistently throughout the season. The variable patterns indicates that making predictions about harvest numbers and probabilities based on changing weather conditions and habitat use is not straight-forward.

Weather did play a measurable role, but the effect of moon phase was a stronger predictor of the probability of being harvested on farmland. Moon phase, together with the effect of day of week, were also strong predictors of hunter effort and overall harvest numbers. In predator-prey relationships an increased visible fraction of the moon is related to increased hunter success (Theuerkauf *et al.* 2003; Cozzi *et al.* 2012). I found increased hunter effort and increased probability of being harvested on farmland during full moon (see paper III, Fig. 2). I also found and increase in the total harvest numbers during full moon, but the effect was not consistent through the season. Hunters focus their activity on farmland during full moon, and as a full moon provides

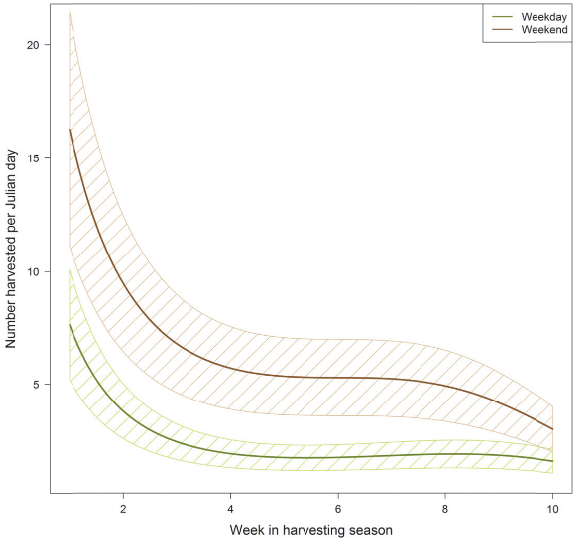

Fig. 7. The total daily harvest numbers of red deer through the harvesting season for the categories weekday (green) and weekend (brown).

increased visibility, it is therefore likely that red deer may spend less time in open habitats like farmland during full moon due to increased risk of being detected (Newhouse 1973). Hunter effort was also markedly increased during weekends as compared to weekdays, and the same relationship was found for total harvest numbers. However, towards the end of the season harvest numbers on weekends and weekdays became more equal (Fig. 7), while the higher hunter effort during weekends persisted. The decrease in harvest numbers during weekends probably reflects a depletion of available animals towards the end of the season. As a learning effect has been documented in how ungulates respond to humans (Geist 1971; Dwyer 2004), the decreased numbers could also be influenced by the red deer increasing their vigilance due to learning. This learning effect is suggested to operate differently between sexes, and to increase with age (Ciuti *et al.* 2012). I therefore expected a higher probability for young, inexperienced deer to be harvested on farmland. Early in the season, yearlings had the highest probability of being harvested on farmland, while the same was apparent for calves towards the end (see paper III, Fig. 3). As fewer yearlings were harvested late in the season, this pattern was consistent with learning, but we cannot rule out depletion or altered hunter preference towards the end of the season. The observed behaviour may yield unintentional harvesting selection, as found in red grouse (Bunnefeld *et al.* 2009).

Hunter selection and long-term trends (paper IV)

The red deer population providing the basis for analyses in paper I, II and III is mainly hunted for meat, and not for trophies (Milner *et al.* 2006). Both hunting for meat and trophies should impose selection pressures on the population and could potentially have large impacts on demographics and life-history traits. These two contrasting hunter aims are expected to produce different selective pressures (Milner *et al.* 2006; review in Mysterud 2011). I therefore wanted to investigate patterns of hunter selection and long-term trends in trophy size in a trophy hunting culture, to be able to compare, and to see if trophy harvesting can be sustainable. Today, the common view is that trophy harvesting causes sufficient directional selection on trait size for an evolutionary response to take place (Allendorf & Hard 2009). As trophy hunters target the traits they actually desire, evolution towards smaller trophies is expected if the trait is heritable and adequate genetic variance is underlying the trait. Even though undesirable effects of trophy harvesting have been demonstrated in mountain sheep (Coltman *et al.* 2003; Garel *et al.* 2007), a number of factors connected to these populations (listed in the Introduction) allows for uncertainty about the wider occurrence of reductions in trait size. Series of harvest records spanning century-long time scales had not yet been analysed to look for long-term trends in trophy size when paper IV was published (but see the recent publication by Monteith *et al.* 2013).

Hungary has a long tradition of trophy harvesting, and actively manages the red deer population with the purpose of increasing the potential for large trophies, e.g. through compensatory culling, the selective shooting of poor-quality males at young age while saving trophy stags until trophy culmination (allowing them to reproduce; Csik 1902; Széchenyi 1948; Mysterud & Bischof 2010). Earlier studies have shown that hunter selection is age-specific for antler- and body size by comparing different hunting methods or categories of hunters (Martinez *et al.* 2005; Mysterud, Tryjanowski & Panek 2006; Torres-Porras, Carranza & Perez-Gonzalez 2009), but there is limited knowledge about how these patterns may vary in space and time. In Hungary, local hunters are expected to take care of the compensatory culling, while foreign trophy stalkers pay to harvest the large trophies. Even though foreign trophy stalkers as expected harvested a larger proportion of prime-aged stags (see paper IV, Fig. 2), and overall larger age-specific stags than local hunters (2.7% larger prime-aged stags),

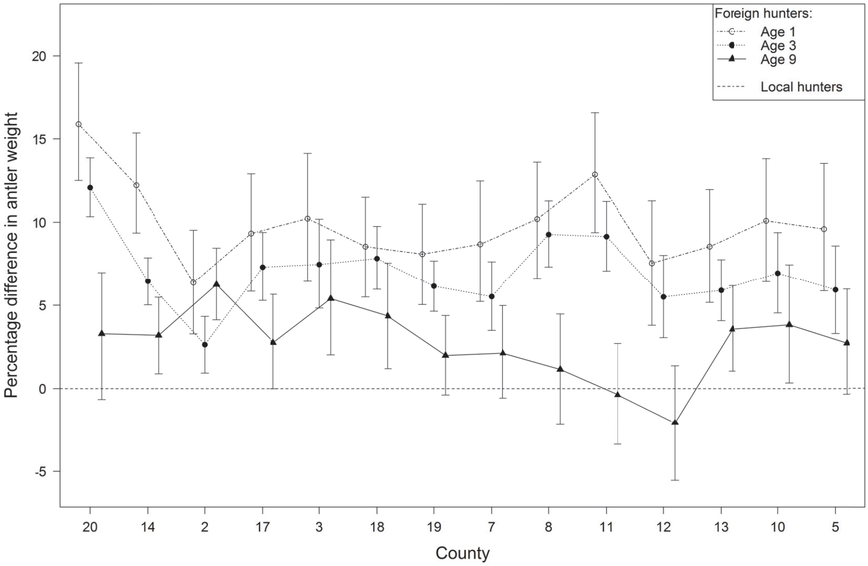

Fig. 8. Spatial variation in the percentage difference in the selection of antler size for foreign trophy hunters (points with corresponding 95 CI) compared to local hunters (dashed line). Differences are predicted for 1 (open circles), 3 (closed circles) and 9 year-old males (triangles). The red deer counties with the highest number of harvested stags start on the left.

the size pattern was not consistent in space and time. Comparing foreign and local hunters I found large variation in age-specific hunter selection for antler size, both between counties (14 counties; Fig. 8) and among years (1973-2008; see paper IV, Fig. 4). This provides evidence that hunter selection is more variable than earlier assumed. More variation in selection for a given trait will weaken the directional selection and the potential for evolutionary change, giving room for other factors such as environmental variation to affect the targeted trait.

When investigating long-term trends (1881-2008) in trophy size, three specific hypotheses were formed: The trophy hunting depletion hypothesis, stating that directional selection for large size will cause an evolutionary change towards smaller size with no potential for recovery (Coltman *et al.* 2003); the restricted trophy hunting hypothesis, which states that management regulations are sufficient to counter the potential negative effects of trophy harvesting, leading to stable trophy sizes over time (Mysterud & Bischof 2010); and the hunting pressure hypothesis, stating that heavy harvesting pressure will lead to smaller

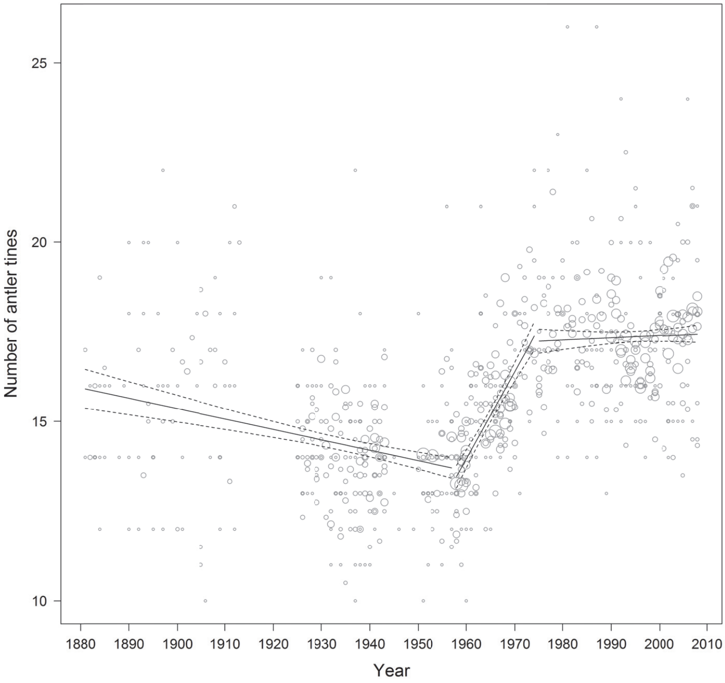

Fig. 9. The predicted pattern of number of antler tines from red deer males shown in trophy exhibitions in Hungary from 1881-2008. Points represent the mean trophy size for each county and year, and the size of the points represents the relative amount of observations used to calculate each mean.

trophy sizes, but this is due to changes in age structure, and not depletion, meaning that the population can recover from declines if harvesting pressure is relieved (Vanpé *et al.* 2007). In contrast to the common view (Allendorf *et al.* 2008; Allendorf & Hard 2009), I found no clear evidence of a long-term negative trend in red deer trophy size over more than a century. The pattern found was divided into three distinct periods with different trophy size trends; a decrease from 1881-1958, followed by an increase from 1958-74 and a levelling off from 1974-2008 (Fig. 9). As trophy size was able to recover after the initial decline, this suggests no depletion of the genes underlying large trophy size, but rather that the changes observed are caused by variable harvest pressure due to changes in management rules resulting in altered (younger) age-structure in the male population of red deer (see Discussion in paper IV for more details on how the management rules varied).

As antler development is dependent on environmental variables and nutritional quality (Frank & Slatkin 1992; Kruuk *et al.* 2002), we cannot rule out the possibility for other factors driving the observed patterns in trophy size. Climate, land use change and population density are known to affect antler development (Pélabon & van Breukelen 1998; Mysterud *et al.* 2005), but such data covering the large geographical area and the long time scale used were not available. Data on mean annual temperature from Budapest was obtained from 1901-2008, but this area may not be representative for the whole of Hungary. Yet, incorporating these data into the analyses did not alter the observed pattern. Also, the population has increased dramatically over the last 50 years. Over the same period land use also changed (Csányi 1997), with increased afforestation leading to new areas for red deer establishment. Thus, even though density has increased, the increase may be less dramatic than the impression given by the population numbers, as the range expanded simultaneously.

CONCLUSIONS AND FUTURE PERSPECTIVES

This thesis provides novel insight about the behavioural mechanisms underlying space use and how this affects harvesting vulnerability and thus also selectivity on different spatial and temporal scales in red deer. At the within-home range scale (paper I), the use of open habitats with more forage but higher risk of being detected by hunters, and covered habitats providing shelter from weather and predators but less forage, varied in relation to time of day/activity levels and habitat availability (functional response), and the strength of the functional response varied with seasons. This pattern, together with the functional response, indicates that anti-predator behaviour together with a behavioural response to climate (thermoregulation and energy expenditures) determines the space use, as forage characteristics do not change over such short time spans as day and night. If the higher risk taken by more extensive use of open habitats with access to greater forage abundance and quality actually cause increased weight gain and growth, remains to be tested. At the home range scale (paper II), the comparison of multiple temporal scales allowed the distinction of direct (e.g. thermoregulatory) and indirect effects (through plant growth) of climate on red deer behaviour. Local climate and habitat composition influenced red deer activity on all temporal scales, but the effect of local climate was strongest on long temporal scales, indicating that indirect climatic effects operating through plant quality and quantity are of higher importance in determining home range size. With the possibility of disentangling the direct and indirect climatic effects, we gain a broader understanding of the effect of climate on behavioural responses such as movement.

Knowledge about the environmental factors determining animal behaviour identified in paper I and II was used to investigate how weather and space use interact in determining harvesting vulnerability and hunter selection (paper III). The results show that making predictions about harvest vulnerability based on prevailing weather and space use is not straight-forward. However, 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 & Østbye 1999). I also found use of covered and open habitats consistent with anti-predator behaviour during moonlit nights, and learning effects may play a role for age-specific harvesting vulnerability in open habitats. However, for the latter, depletion of yearlings and/or hunter preference cannot be ruled out. A depletion of accessible animals was also apparent when comparing harvest numbers during weekends and weekdays through the season, as the in general higher number of red deer harvested during weekends approached the number harvested during weekdays towards the end of the hunting season. 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. My results show that interaction effects of weather and space use on hunter behaviour are complicated, and may be less important than hunter preference and quotas in determining hunter selection and harvest off-take.

Large spatiotemporal variation in hunter selection was also found for harvested populations in Hungary (paper IV). Analyses of hunter selection and long-term trends in trophy size allowed for more insight into how management of ungulate populations under heavy trophy harvesting can be sustainable, and I propose a set of factors to be used as a basis for evolutionary enlightened management (sensu Ashley *et al.* 2003); compensatory culling (Mysterud & Bischof 2010), spatial (Tenhumberg *et al.* 2004) and temporal refuges (paper IV), saving stags until prime-age and trophy culmination allowing reproduction (Csik 1902; Széchenyi 1948; Apollonio, Andersen & Putman 2010) and also redirection of hunter preference through progressively higher prices for larger trophies or through fines or penalties for mismanagement (shooting stags of the wrong size). Distinguishing plasticity or environmental effects from evolutionary responses in phenotypic traits is challenging (Allendorf & Hard 2009). Though clearly it is easy to see the limitations of using data from trophy exhibitions, they are at least likely to yield some insight into the long-term sustainability of hunting (Pelletier, Festa-Bianchet & Jorgenson 2012). As such data represent the upper end of the size scale, the magnitude and changes of trait variation are not available. However, directional selection also decreases the trait variance (Shnol & Kondrashov 1993), meaning that a decline in size should also be apparent for trophy exhibition data if directional selection from trophy harvesting was the primary driver of antler size development.

The dramatic political changes in Europe during 1881-2008 has markedly affected game management in Hungary (Csányi 1997), and the changes in hunting pressure resulting from this is likely to be the driver behind the long-term patterns observed. Currently, new management acts have been issued, e.g. with local hunters gaining increased access to trophy stags, which may cause an increase in harvesting pressure. A limitation of currents studies on trophy size development is that the phenotypic variation found is rarely linked to genetics. A broader understanding of the genetics involved in antler size development would allow more relevant monitoring of trophy size trends in ungulate populations from an evolutionary perspective. Future studies should therefore continue to monitor harvested ungulate populations, and strive to identify the underlying genetics behind antler size, as well as collect detailed data on climate, density and land use change. Also, even though Norway has a hunting culture focused on meat and recreation, trophy harvesting is advancing (Andersen *et al.* 2011). The knowledge gained from trophy harvesting cultures such as Hungary is important to be able to predict future scenarios and adjust management rules to ensure sustainable harvesting also in other countries under change.

ACKNOWLEDGEMENTS

I am very grateful to Atle Mysterud, Leif Egil Loe and Jostein Gohli for constructive and valuable comments on previous drafts of this synthesis. I also wish to thank Sándor Csányi for providing distribution maps over red deer harvest data and medals in Hungary.

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Ecology, 90(3), 2009, pp. 699–710

Temporal scales, trade-offs, and functional responses in red deer habitat selection

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Abstract. Animals selecting habitats often have to consider many factors, e.g., food and cover for safety. However, each habitat type often lacks an adequate mixture of these factors. Analyses of habitat selection using resource selection functions (RSFs) for animal radiotelemetry data typically ignore trade-offs, and the fact that these may change during an animal's daily foraging and resting rhythm on a short-term basis. This may lead to changes in the relative use of habitat types if availability differs among individual home ranges, called functional responses in habitat selection. Here, we identify such functional responses and their underlying behavioral mechanisms by estimating RSFs through mixed-effects logistic regression of telemetry data on 62 female red deer (*Cervus elaphus*) in Norway. Habitat selection changed with time of day and activity, suggesting a trade-off in habitat selection related to forage quantity or quality vs. shelter. Red deer frequently used pastures offering abundant forage and little canopy cover during nighttime when actively foraging, while spending much of their time in forested habitats with less forage but more cover during daytime when they are more often inactive. Selection for pastures was higher when availability was low and decreased with increasing availability. Moreover, we show for the first time that in the real world with forest habitats also containing some forage, there was both increasing selection of pastures (i.e., not proportional use) and reduced time spent in pastures (i.e., not constant time use) with lowered availability of pastures within the home range. Our study demonstrates that landscape-level habitat composition modifies the trade-off between food and cover for large herbivorous mammals. Consequently, landscapes are likely to differ in their vulnerability to crop damage and threat to biodiversity from grazing.

Key words: Cervus elaphus; *habitat selection; large mammals; mixed-effects logistic regression; Norway; red deer; resource selection functions; resource use; trade-offs; ungulates.*

INTRODUCTION

Habitat selection is an important component of the ecology of a species (Rosenzweig 1981), and is frequently defined as the disproportionate use of habitat types (Johnson 1980). Four hierarchical orders of selection are identified based on what spatial scale use and availability are measured (Johnson 1980, Senft et al. 1987). At the within-home-range scale, habitat selection is usually linked to the animal's daily foraging and resting rhythms, in contrast to selection of home ranges at broader scales, which is often linked to dispersal processes or seasonal migrations (Morris 1987). In the following, we focus on the within-home-range scale. When animals choose a habitat, they often have to consider many factors, such as forage quality and availability, shelter, and potential predators (Sih 1980, Werner et al. 1983). Each habitat type may not always contain an adequate mixture of these factors (Orians and Wittenberger 1991). The resulting choice of habitat is thus the outcome of trade-offs between the costs and benefits perceived by the animal (Lima and Dill 1990, Mysterud and Ims 1998). A common trade-off often faced by many large mammals takes place when exposed habitats provide the best forage, while closed habitats provide shelter against harsh weather and/or predators. How the trade-off affects the individuals may vary with season, time of day, and weather conditions, and also with the animal's sex, age, and daily activity (Beier and McCullough 1990, Manly et al. 2002).

One of numerous methods available for investigating habitat selection is resource selection functions (RSFs), defined as any function proportional to the probability of use of a resource unit or area by an animal (Manly et al. 2002). These sets of methods, commonly logistic regression (Johnson et al. 2000, Boyce et al. 2002, Nielsen et al. 2002, Boyce et al. 2003), have been applied in studies of habitat selection across a diverse range of

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Manuscript received 26 March 2008; revised 3 June 2008; accepted 16 June 2008. Corresponding Editor: T. J. Valone.

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species, from Pileated Woodpeckers (*Dryocopus pileatus*; Lemaitre and Villard 2005) to grizzly bears (*Ursus arctos*; Nielsen et al. 2002). Within an animal's home range, locations for resource use by the individual are averages over the period when the data are collected, and the typical advice given is that the selection times should be kept as short as possible because the habitats may change (Manly et al. 2002), e.g., between seasons. However, such approaches ignore how trade-offs may change during an animal's daily foraging and resting rhythm on a more short-term basis. This may cause the estimates given by the overall RSFs to be less informative, because the selection of a resource will differ contingent on the availability of that resource (Mysterud and Ims 1998, Mauritzen et al. 2003).

The time budgets of ruminants are (outside of rutting season) mainly composed of alternating foraging and rumination/resting bouts, the duration of which is driven mainly by diet quality (Gillingham et al. 1997). The foraging bouts more often take place in open habitats where forage is abundant, whereas rumination/resting bouts are more often carried out in covered habitats with less forage due to shading of plants (Mysterud et al. 1999). It is also common to use more open forage-rich habitats during darkness, and covered habitats with less forage during daylight (Armstrong et al. 1983, Beier and McCullough 1990). Surprisingly few recent habitat selection studies using RSFs have taken these insights into account by separating data sets in relation to time (day vs. night) or state of activity (resting vs. foraging), despite that this is a rather old biological insight. We test the hypothesis (H_1) that temporal scale is important for habitat selection, predicting a higher selection of habitats with more cover during daylight, and higher selection of open habitats rich in forage during nighttime.

A related problem occurs if animals use different habitats for different activities or time periods, and because home ranges often differ in the composition of habitat types due to landscape level variation, the relative use of a given habitat type will change between individuals due to variable availability, termed a functional response in habitat selection (Mysterud and Ims 1998). Only a few studies have measured functional responses in habitat selection after this was identified (Boyce et al. 2003, Mauritzen et al. 2003, Osko et al. 2004, Gillies et al. 2006, Hebblewhite and Merrill 2008). However, none of these studies explored the behavioral mechanisms by which this arises at the individual level; they only showed a change in selection with changing availability. One extreme is that animals always spend a fixed proportion of their time in a given habitat type, regardless of availability. In contrast, the traditional theoretical framework of habitat selection vs. avoidance assumes that habitat use is proportional to availability (with a proportionality constant >1 indicating selection and <1 avoidance). However, the real world is more complex, with forest habitats providing cover but typically also some forage, although usually less than, for example, pastures. We therefore expect that habitat use is neither constant nor proportional, but falls between these two extremes. We term this the real-world trade-off hypothesis (H_2), and predict increasing selection of pastures (i.e., not proportional use), but reduced time spent in pastures (i.e., not constant time use), with lowered availability. Further, no study has addressed possible seasonal variations in the strength of functional responses in habitat selection. The seasonal environment imposes large variations in the distribution of forage and cover through the year, which is likely to affect the relative amount of resources between habitat types. From the seasonal trade-off hypothesis (H_3), we expect the functional response to be more pronounced during seasons with larger differences between forage quality and/or quantity in covered and open habitats.

Here, we employ mixed-effects logistic regression models of RSFs to test these hypotheses (H_{1-3}) regarding temporal scales (activity, time of day, season), trade-offs, and functional responses in habitat selection using new data on 62 GPS- or VHF-collared female red deer (*Cervus elaphus*) in Norway. Red deer frequently use pastures offering abundant forage and no canopy cover, while spending much of their time in various types of forested habitats with less forage, but more cover. This case is thus ideally suited for testing these hypotheses regarding individually and seasonally variable trade-offs and functional responses in habitat selection.

MATERIALS AND METHODS

Study area

The study area is located in the western part of southern Norway, and consists of three regions in Sogn og Fjordane county (Fig. 1): (1) Nordfjord (the municipalities Gloppen and Stryn), (2) Sunnfjord (Jølster, Flora, Naustdal, Førde, Gaular, Askvoll, and Fjaler), and (3) Ytre Sogn (Balestrand, Høyanger, Hyllestad, and Solund). The vegetation is mostly in the boreonemoral zone (Abrahamsen et al. 1977). Natural forests are dominated by deciduous forest (predominately birch *Betula* sp. and alder *Alnus incana*) and pine forest (*Pinus sylvestris*), with juniper (*Juniperus communis*), bilberry (*Vaccinium myrtillus*), and heather (*Calluna vulgaris*). Norway spruce (*Picea abies*) has been planted on a large scale. Agricultural areas are normally situated on flatter and more fertile grounds in the bottom of valleys, mostly as pastures and meadows for grass production dominated by timothy (*Phleum pratense*). The topography is characterized by steep hills and mountains, valleys, streams, and fiords. Precipitation and temperature generally decline from coast to inland, whereas depth and duration of snow cover increase (Langvatn et al. 1996). Snow cover is normally present at the coast in January and February, but highly variable among years and with altitude (Mysterud et al. 2000).

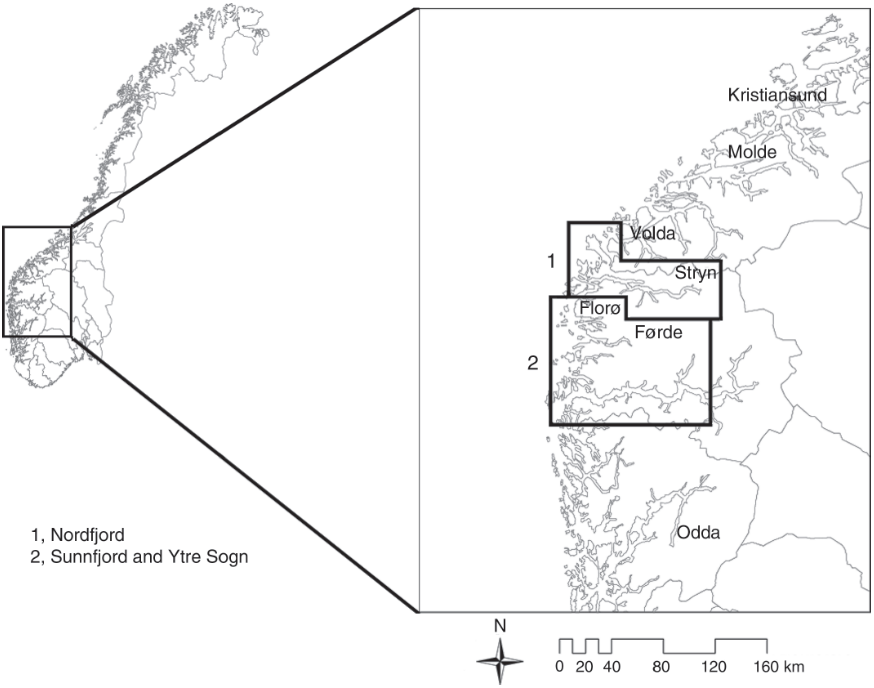

FIG. 1. Map of the study area situated in the western part of southern Norway. Boxes represent the different regions inhabited by the red deer (*Cervus elaphus*) in this study.

Red deer data

The data on red deer derive from 40 female red deer marked with GPS (Global Positioning System) collars in the Sunnfjord and Ytre Sogn region, and 22 red deer marked with ordinary VHF (Very High Frequency) collars in the Nordfjord region. All animals were caught by darting on winter feeding sites, after a procedure approved by the national ethical board for science ("Forsøksdyrutvalget").

Sunnfjord region.—In the area of Sunnfjord and Ytre Sogn (hereafter termed Sunnfjord), the red deer were caught and fitted with Televilt Basic "store-on-board" GPS collars or Televilt Basic GPS collars with GSM option (for transfer of data via cell phone network; Televilt TVP Positioning AB, Lindesberg, Sweden) in January and February 2005 and March 2006. All of the collars were programmed to record a position once every hour. After approximately 10 months, we released the collars with a drop-off mechanism (tracking period 6–12 months; see Appendix A: Table A1). All locations taken during the first 24 hours after marking were deleted, and all positions where the animals had moved at a speed of more than 40 km/h and more than 10 km between fixes were removed (0.5% of the locations taken with hourly intervals), because they most likely are GPS errors. As this study focuses on habitat selection at the within-home-range scale, removing these outliers should not bias results.

Nordfjord region.—Red deer in Nordfjord were fitted with Televilt VHF collars (Televilt TVP Positioning AB, Lindesberg, Sweden) during winters in 2001–2005. We tracked 22 female red deer with functional collars in 2006 once a day during two periods in winter (15 February–1 March and 15–31 March 2006) and two periods in summer (13 June–7 July and 31 July–7 August 2006). At least three bearings were taken from different observer positions for every individual, to obtain a more precise position of the deer. We aimed for the shortest possible time between each bearing, and the difference between the angles always exceeded 20°. If we obtained visual observations of individuals, the position was located with a GPS. On average, 29 positions were obtained for each animal each season. Activity was determined by a mercury switch in the collar, based on different pulse rates (0.6-s pulse rate when active and 1.2 s when inactive). These sensors have been shown to be >95% accurate in distinguishing active from inactive behavior (Beier and McCullough 1988, Hansen et al. 1992). Most of the radio-tracking was done from or close to the road. The route was changed daily after a random schedule, to vary the time of day when each individual was located, and we aimed to obtain one-third of the positions after darkness (this resulted in

72.8% of locations during light, 7.8% during civil twilight, and 20.0% during darkness). The resulting data were processed in LOAS 4.0b (Ecological Software Solutions, Florida, USA; *available online*).[5] We estimated individual locations together with associated error ellipses, using standard triangulation techniques (White and Garrott 1990) on the bearings obtained for each animal and day. As a first control, the resulting positions were plotted onto digital land resource maps to check if any of the estimated positions ended up in the sea or other unlikely habitat categories. This was never the case. The sizes of the error ellipses were generally small (mean 10.65 ha, 95% CI 8.70–12.60 ha, median 1.85 ha, range 0.00–675.66 ha), and all locations were included in the analysis (Appendix B). For comparison, the mean size of habitat patches with the VHF collared individuals' 100% seasonal home ranges (minimum convex polygon) was 4.41 ha (95% CI 3.62–5.20 ha, median = 0.44 ha, range 0.00–436.00 ha).

The GPS collars did not contain activity switches, while the VHF collars did. We expect that some of the effect of light conditions (light, civil twilight, dark) on habitat selection will occur due to differences in activity between night and day. To check the correspondence between light intensity and the probability of being active, we used the VHF animals to fit a logistic regression model with activity (active, rapid VHF pulses; passive, slow VHF pulses) as a response variable and light as the predictor variable. We used the result of the model to draw inferences on effect of activity (using light as a proxy) also for GPS collared deer.

Habitat types

Habitat types were derived from digital land resource maps provided by the Norwegian Forest and Landscape Institute, with scale 1:5000. The digital resource maps were divided into five habitat types, by merging of habitat classes from the original maps. Availability and use of lakes, sea, and uncharted areas (habitat type 5) were eliminated from all analyses, leaving four used and available habitat types: pastures, forest of high productivity, forest of low productivity, and "other" (see Appendix C for a brief description of the habitat types). The maps were rasterized in ArcMAP 9.2 (ESRI 2006), with a resolution of 50 × 50 m. The raster maps were then converted to ASCII for use in the analyses.

Correcting for potential GPS bias

Data obtained with GPS are prone to variation in fix-success rates and location errors (D'Eon and Delparte 2005, Graves and Waller 2006). The median location error for our GPS collars was 12 m, comparable to earlier reports (D'Eon and Delparte 2005). As most habitat maps have similar or lower accuracy, location errors may be of less concern in habitat selection studies. Variable fix rates and missing data are probably a larger source of potential bias and error in GPS data (D'Eon 2003, Frair et al. 2004). A fix rate <100% may bias selection estimates if locations are missed in some habitats more often than in others (D'Eon and Delparte 2005). This is particularly a concern when comparing open habitats (such as pastures) with covered habitats (forests), because canopy cover is shown to have an impact on location acquisition in GPS collars (D'Eon et al. 2002). The GPS collars worn by red deer in this study achieved an average fix rate of 91% (range 77–98%; see Appendix A: Table A1). We used iterative simulation to correct for possible GPS bias in the red deer GPS data prior to analyzing habitat selection (Frair et al. 2004). Details on how this was done are described in Appendix A, together with analysis of both corrected and uncorrected GPS data.

Statistical analysis

Resource selection functions (RSFs) were estimated using use–availability logistic regression (design III data; Boyce et al. 2002, Manly et al. 2002) with random intercepts for each individual in each season to account for differences in sampling intensity (Wood 2006:310–315). The probability of use was thus modeled by the equation

$$P_{\text{use}} = \frac{\exp(\beta_0 + \beta_1 x_{1ij} + \beta_2 x_{2ij} + \cdots + \beta_n x_{nij} + \lambda_{0j})}{1 + \exp(\beta_0 + \beta_1 x_{1ij} + \beta_2 x_{2ij} + \cdots + \beta_n x_{nij} + \lambda_{0j})} \tag{1}$$

where observations $i = 1 \ldots n$ are clustered within strata $j = 1 \ldots m$; i.e., locations for each individual per season, β_0 is the mean intercept, β_n are the fixed-effect coefficient estimates for the covariates x_n, and γ_{0j} is the random intercept, which is the difference between the mean intercept β_0 for all groups, and the intercept for group j (Skrondal and Rabe-Hesketh 2004). The random intercept adjusts the overall average probability of use, which depends on the number of locations for each individual (in our case this varied among individuals and seasons). Models with random intercepts were fitted using the library lme4 (Bates 2007) implemented in R (R Development Core Team 2008). The binary response variable in the model was used vs. available pixels. Used pixels corresponded to bihourly (every two hours) locations for the GPS-collared individuals (due to computational constraints, hourly locations could not be used) and daily locations for the VHF-collared individuals. Available pixels corresponded to a total of 2000 random pixels for the GPS-collared individuals and 1000 random pixels for the VHF-collared individuals, sampled within individual 100% seasonal home ranges (minimum convex polygon). The model included the fixed effects habitat (pasture, forest of high productivity, forest of low productivity, and other [marshland, mountains, and bare rock]), season (winter, 1 December–31 March; spring, 1 April–31 May;

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[5] ⟨http://www.ecostats.com/software/loas/loas.htm⟩

TABLE 1. Summary of mixed-effects logistic regression model for predicting habitat selection in 40 GPS-collared female red deer (*Cervus elaphus*) in Sunnfjord, Norway.

			HPD interval bounds	
Variable	β	SE	Lower	Upper
Intercept	1.167	0.134	0.901	1.431
Habitat†				
Other	−1.902	0.115	−2.135	−1.685
Productive forest	−1.016	0.113	−1.254	−0.811
Low-productive forest	−1.173	0.114	−1.399	−0.946
Season‡				
Autumn	0.703	0.168	0.358	1.024
Spring	1.346	0.168	1.008	1.664
Winter	0.002	0.183	−0.368	0.346
Light intensity§				
Light	−1.804	0.033	−1.867	−1.742
Civil twilight	−0.569	0.048	−0.662	−0.476
Habitat × season				
Other × autumn	−0.403	0.134	−0.649	−0.121
Productive forest × autumn	−0.360	0.132	−0.604	−0.083
Low-productive forest × autumn	−0.533	0.133	−0.782	−0.258
Other × spring	−1.779	0.134	−2.029	−1.503
Productive forest × spring	−1.392	0.131	−1.638	−1.125
Low-productive forest × spring	−1.859	0.133	−2.116	−1.596
Other × winter	−0.323	0.154	−0.611	−0.010
Productive forest × winter	−0.502	0.150	−0.770	−0.186
Low-productive forest × winter	−0.827	0.151	−1.103	−0.512
Habitat × light intensity				
Other × light	1.767	0.038	1.695	1.842
Productive forest × light	2.061	0.035	1.991	2.130
Low-productive forest × light	2.070	0.040	1.995	2.150
Other × civil twilight	0.596	0.058	0.486	0.712
Productive forest × civil twilight	0.688	0.053	0.581	0.787
Low-productive forest × civil twilight	0.730	0.061	0.606	0.842
Pasture availability × pasture use	−1.921	0.269	−2.474	−1.409
Pasture availability × pasture use × season				
Pasture availability × pasture use × autumn	−0.125	0.332	−0.765	0.545
Pasture availability × pasture use × spring	−2.344	0.319	−2.975	−1.726
Pasture availability × pasture use × winter	−1.270	0.405	−1.980	−0.396

Notes: The model includes random intercepts for individual red deer each season (idseason; SD = 0.468 [HPD interval 0.423–0.535]). HPD intervals are the highest posterior density intervals (Plummer et al. 2007). Sample sizes are the number of locations: $N_{\mathrm{obs}} = 138\,876$ observed locations from GPS collars; $N_{\mathrm{av}} = 133\,865$ available locations drawn at random from within the individual home ranges.

† Reference = pastures.

‡ Reference = summer.

§ Reference = dark.

summer, 1 June–15 August; autumn, 16 August–30 November), and light condition (light, civil twilight, and dark), as well as the interaction between habitat and season, and between habitat and light condition. Light conditions were based on hours of sunset, civil twilight, and sunrise for the area, obtained from the U.S. Naval Observatory (data *available online*).[6] References for categorical fixed effects are given in Tables 1 and 2. To test for a functional response in the use of pastures, we estimated a fixed effect of pasture availability for the use of pasture pixels. This was implemented as the interaction between the Boolean variable "habitat = pasture" and the arcsine square-root-transformed proportion of pastures in each individual's seasonal home range. This was also entered in interaction with season, allowing the functional response to vary over the year.

From the coda library (Plummer et al. 2007) implemented in R, we used 10 000 Markov Chain Monte Carlo (mcmc) samples and 95% Highest Posterior Density intervals (HPD intervals) to evaluate the properties of the individual coefficients (Bates 2006). The HPD intervals yields intervals for the individual coefficients in the mixed models from the mcmc samples, and from this we can evaluate if the coefficients are significantly different from 0.

To illustrate red deer habitat selection, we estimated log odds ratios for habitat use on the population level, for each combination of habitat, season, and light intensity. All log odds ratios were calculated relative to the use of pastures in summer during daylight, and for

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[6] ⟨http://aa.usno.navy.mil⟩

TABLE 2. Summary of the mixed-effects logistic regression model for predicting habitat selection in 22 VHF-collared female red deer in Nordfjord, Norway.

Variable	β	SE	HPD interval bounds	
			Lower	Upper
Intercept	−1.970	0.566	−3.102	−0.911
Habitat†				
Other	−1.818	0.624	−2.982	−0.577
Productive forest	−1.549	0.575	−2.609	−0.373
Low-productive forest	−1.420	0.606	−2.559	−0.226
Season‡				
Winter	−0.528	0.688	−1.768	0.959
Light intensity§				
Light	−1.049	0.255	−1.549	−0.563
Civil twilight	−0.103	0.447	−1.049	0.696
Habitat × season				
Other × winter	0.143	0.717	−1.359	1.478
Productive forest × winter	0.586	0.692	−0.862	1.870
Low-productive forest × winter	0.032	0.708	−1.381	1.444
Habitat × light intensity				
Other × light	1.040	0.365	0.378	1.777
Productive forest × light	1.218	0.271	0.678	1.725
Low-productive forest × light	1.075	0.333	0.397	1.715
Other × civil twilight	0.226	0.578	−0.903	1.390
Productive forest × civil twilight	0.148	0.476	−0.779	1.099
Low-productive forest × civil twilight	0.104	0.551	−0.952	1.203
Pasture availability × pasture use	−5.506	2.006	−9.258	−1.567
Pasture availability × pasture use × season				
Pasture availability × pasture use × winter	3.879	2.262	−0.627	8.164

Notes: The model includes random intercepts for individual red deer each season (idseason; SD = 2.2×10^{-5} [HPD interval 4.3×10^{-12}–1.0×10^{-7}]). HPD intervals are the highest posterior density intervals (Plummer et al. 2007). $N_{obs} = 1284$ observed locations from GPS collars; $N_{av} = 42\,571$ available locations drawn at random from within the individual home ranges.

† Reference = pastures.

‡ Reference = summer.

§ Reference = dark.

the average availability of pastures (termed baseline). Population-level fitted log odds and odds ratios were calculated as follows. Let **x** denote a row in the fixed-effects design matrix, i.e., a vector of covariate values characterizing a given pixel, and let $\boldsymbol{\theta}_j$ be the *i*th mcmc sample from the posterior distribution of the parameter vector. Then $\mathbf{x}\ \boldsymbol{\theta}_j$ is the *i*th sample of the fitted log odds of use for this pixel, for the average individual deer. Similarly, samples of log odds ratios are calculated as $(\mathbf{x} - \mathbf{x}_0)\ \boldsymbol{\theta}_j$, where $\mathbf{x}_0$ characterizes the baseline pixels for comparison. Interval estimates for fitted odds ratios were based on 10 000 mcmc samples from the posterior distribution of the parameters and random effects. The 95% HPD intervals were calculated from the resulting mcmc samples of fitted values (Bates 2006).

The functional response was visualized by calculating the population-level log odds ratios of use of pasture pixels, in the same manner as previously stated, but with baseline being during darkness and with average seasonal availability of pastures. Group-level estimates (i.e., for the "group" of pixels available to an individual deer) were calculated as follows. Let **z** denote a row in the random-effects design matrix (characterizing a baseline pixel for a specific individual), and let $\mathbf{b}_i$ be the *i*th sample of the random effects. Then $\mathbf{x}\ \boldsymbol{\theta}_j + \mathbf{z}\ \mathbf{b}_i$ is the *i*th sample of the fitted log odds of use for this pixel by this individual. Individual-specific odds ratios were then calculated as $(\mathbf{x} - \mathbf{x}_0)\boldsymbol{\theta}_j + (\mathbf{z} - \mathbf{z}_0)\mathbf{b}_i$, where $\mathbf{z}_0$ characterizes a baseline pixel (for the same individual) for comparison. To investigate H_2, estimated curves of constant use were added to the figure. It should be noted that these curves may be shifted up or down by an unknown amount, because only relative, not additive, odds may be estimated with use–availability sampling in logistic regression. Proportional use would be represented as horizontal lines (slope = 0).

Results

Temporal scales of habitat selection

The overall selection pattern was quite similar in both regions (Fig. 2, Tables 1 and 2), indicating that results are not due to biases introduced by the method used. Fewer significant variables in Nordfjord most likely originate from the much lower sample size, as estimates are fairly similar (Table 2). The red deer showed substantially higher activity levels during darkness than in daylight, with civil twilight activity levels found in between (Fig. 3). This also indicates that the activity sensors in the VHF collars were reliable, as they were

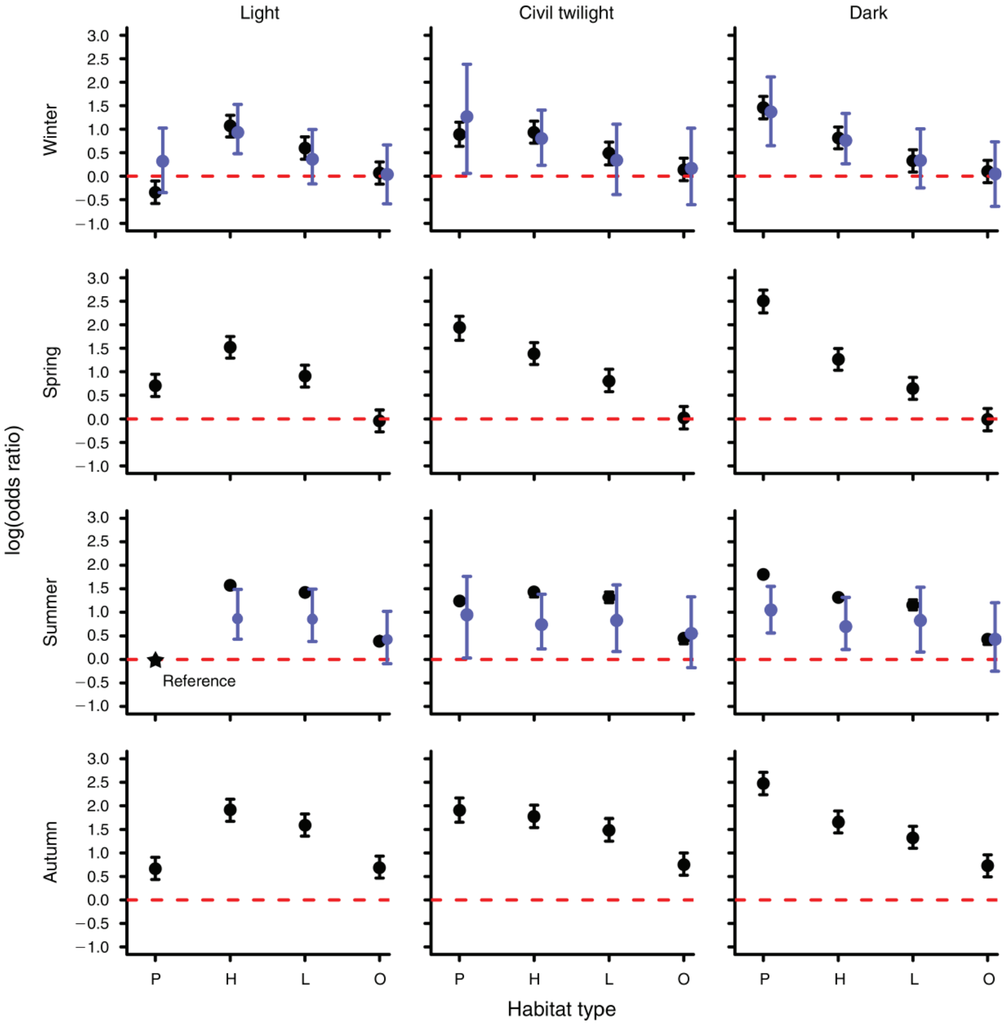

FIG. 2. Comparing habitat selection through different seasons and light intensities for 62 female red deer in Norway. Estimates are log odds ratios ± 95% highest posterior density intervals, where the log odds ratios are calculated relative to selection of pastures in summer during daylight (reference star). The red line specifies the reference level, and values above 0 indicate higher selection of the particular habitat type relative to the reference, whereas values below 0 indicate lower selection. Individuals from Sunnfjord (with GPS collars) are shown in black, and individuals from Nordfjord (with VHF collars) are in blue. The letters P-H-L-O on the *x*-axis indicate the different habitat types: P, pastures; H, high-productivity forest; L, low-productivity forest; O, other.

able to track the expected peaks in activity with changing light intensity.

The red deer showed a very similar pattern of selection during all seasons, when separated for the various light conditions (Fig. 2). As predicted from hypothesis H_1, the main pattern was higher selection for pastures during darkness, and higher selection for forest of high productivity during daylight and less during darkness. During civil twilight, pastures and forest of high productivity were selected on approximately the same level. Seasonal differences in selection consisted of higher selection of pastures in spring and autumn than in the remaining seasons. During summer, forest of low productivity was also somewhat more selected.

Comparing the resource selection functions estimated from the corrected and the uncorrected data set, we found the overall pattern of selection and relationship between selection of habitat types to be quite similar,

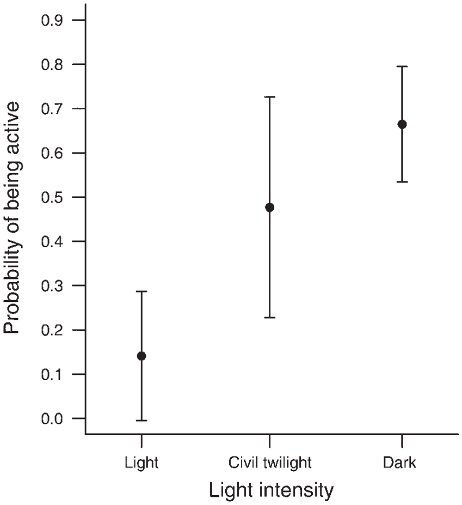

FIG. 3. Probability of being active (mean ± SE) as a function of light condition (light, civil twilight, and dark), for 22 VHF-collared female red deer in Norway. Activity was recorded based on the pulse rate of VHF collars (see *Materials and methods*).

but the log odds ratio of selection was generally lower in the uncorrected data set (Appendix A: Fig. A1).

Functional response in habitat selection

For both regions, the log odds ratio of use of pasture pixels decreased with increasing availability during all seasons (Fig. 4), confirming the presence of functional responses in habitat selection. Selection for pastures was higher when availability was low, and decreased with increasing availability (see Appendix D for an overview of seasonal pasture use for individual red deer). The individuals did spend more time on pastures with increasing availability, but not proportionally more, because the shapes of the log-odds-ratio curves were different from horizontal (proportional use). Also, the log-odds-ratio curves were less steep than the estimated curves for constant use. Due to this, use was neither proportional nor constant with changing availability, but somewhere in between, as predicted by hypothesis H_2. For the Sunnfjord region, the functional response appeared strongest during spring and, consistent with hypothesis H_3, this response was weakest during summer (Fig. 4). This was not the case for the Nordfjord region, where the red deer exhibited the strongest response in summer and weakest in winter. Comparing results from the corrected and uncorrected data sets, we found similar patterns (Appendix A: Fig. A2).

DISCUSSION

Trade-offs are well known to affect animal habitat selection across a diverse range of species (Lima and Bednekoff 1999, Reckardt and Kerth 2007), but relatively few studies have quantified this from animal telemetry data. Using a simulated data set, Gillies et al. (2006) implicitly identified functional responses by identifying individual heterogeneity using random effects. However, individual heterogeneity may also arise from other factors, such as age or reproductive status. Here, we have brought their approach one step further by explicitly modeling the functional responses in habitat selection, with the addition of a fixed term for the interaction between pasture availability and pasture use. Further, we identify the underlying behavioral mechanisms determining habitat selection related to variation in selection over short-term temporal scales. As shown earlier, and consistent with hypothesis H_1, habitat selection changed with light condition and state of activity, which will give rise to a functional response when habitat availability varies between individual home ranges (Mysterud and Ims 1998). We demonstrate that selection of pastures declined with availability. Moreover, for the first time we show that the time spent in a key habitat type was neither constant nor proportional to available area, but somewhere in between (in support of H_2). We also found evidence for seasonal variation in the functional response (H_3), with the trade-off being stronger during seasons when variations between the quality and quantity of forage in covered and open habitats were larger.

Comparing results from the data set corrected for possible GPS bias induced by missing locations and an uncorrected data set, we found very similar results. This may be an indication of a fix rate > 90%, as found in this study, being sufficient for habitat selection studies. However, although this is the case for our study, it may not be similar when working with GPS data from areas with different habitat compositions or from different collar types.

Behavioral mechanism for functional responses

In this study, light intensities throughout the day have been used to infer patterns regarding short-term variation in selectivity. As the GPS collars did not have activity switches, we had to assume that main activity was during darkness and twilight, and that inactivity dominated during daylight. It has been shown several times that red deer (Georgii 1981, Georgii and Schroder 1983, Catt and Staines 1987, Carranza et al. 1991) and many other cervids (Cederlund 1981, Beier and McCullough 1990, Ager et al. 2003) are mainly active during dusk and dawn, and in nighttime (but see Clutton-Brock et al. [1982] for a different activity pattern). We also found evidence for this in the red deer equipped with VHF activity collars in our study (Fig. 3). This supports the assumption that the red deer are primarily active during civil twilight and nighttime, and suggests that the approach of using state of activity and light intensity together are appropriate for our purpose. On the daily scale, we found stronger selection of cover during daylight than in darkness, confirming hypothesis H_1.

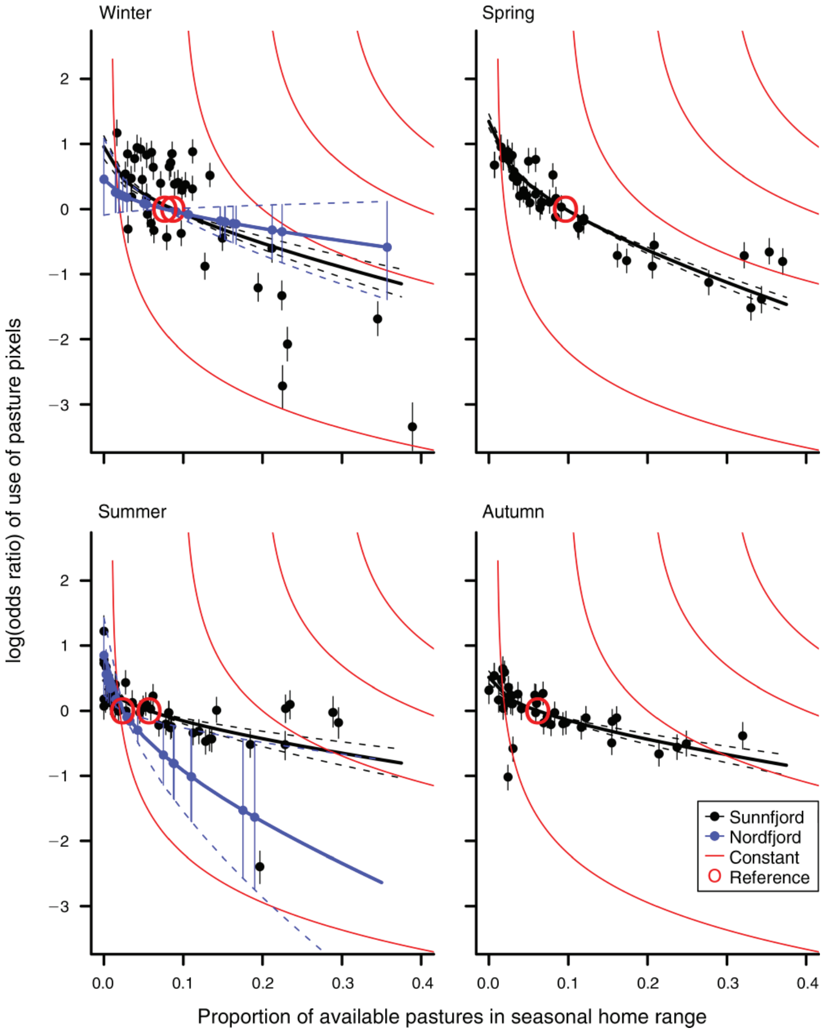

FIG. 4. Functional responses in the selection of pastures for 62 red deer in Norway (Sunnfjord/GPS, black symbols and lines; Nordfjord/VHF, blue symbols and lines). The log odds ratios of the use of pasture pixels are calculated relative to average available pastures in the seasonal home range (red circles) and provide a measure of selection. The points are individual red deer; error bars and the dashed lines represent 95% highest posterior density intervals. Red lines illustrate constant use of pastures; a hypothetical horizontal line (slope = 0) would indicate proportional use of pastures.

Variations in forage characteristics, being important for annual variation, are not expected to induce daily patterns in habitat use, because forage characteristics most likely vary little through the day. This pattern is commonly interpreted as a behavioral response to predator threats in ungulates (reviewed in Mysterud and Østbye 1999). The higher use of covered habitat may also be due to its ability to relieve negative effects from heat and cold stress arising from temperature, wind, and radiation, to lower heat loss resulting from precipitation, and to decrease energy expenditure because of lower snow depth (Parker et al. 1984, Mysterud and Østbye 1999).

Red deer in Norway showed stronger selection for forest habitats (with more cover) in summer and winter than in spring and autumn, when pastures were more frequently selected. Similar selection for covered habitats in summer have also been found earlier in red deer (Carranza et al. 1991) and in Rocky Mountain elk (*Cervus elaphus*) (Boyce et al. 2003). At northern latitudes, there is strong seasonal variation in forage quality and quantity (Clutton-Brock et al. 1982, Albon and Langvatn 1992, Van Soest 1994), and to some extent also in canopy cover in the different habitats (Mysterud and Østbye 1999). Pastures, in our study area mainly meadows with timothy, hold forage of higher quality and abundance relative to forested habitats throughout the year (Albon and Langvatn 1992). However, snow cover leads to increased energy expenditures for movement and inhibits access to forage (Parker et al. 1984). Several studies on ungulates have reported increased use of older forest when snow depth was greater (Armleder et al. 1994, Poole and Mowat 2005, Jenkins et al. 2007), which probably explains the lowered selection of pastures during winter in our study. In summer, although not well quantified, the quality and quantity of forage in the forested areas probably approach those of pastures in summer due to higher productivity, which together with mothers having offspring (at a higher risk of being predated) can explain the higher selection of covered areas during summer. Calves exhibit reduced mobility during this period, and staying in covered habitats could lower the risk of predation on the calves.

Variations in the strength of trade-offs

The red deer in this study exhibited a functional response in selection of pastures, as predicted by hypothesis H_2. This was apparent through all seasons, indicating that they experienced trade-offs involving activities that are spatially segregated and specific to the various habitats. The strength of the trade-off and the functional response varied with both habitat availability and seasons. The time spent on pastures increased with increasing availability, but not in a directly proportional manner, leading to the strength of the trade-off varying with habitat availability driven by landscape-level variability. The seasonal variation in the trade-off may be due to seasonally varying abundance of forage and cover in the different habitats. In autumn and spring, selection of open and covered habitats differed considerably through the day, as adequate cover and highly nutritious forage are rarely found in the same habitat. In contrast, the shifting of habitats through the day was less pronounced during summer and winter. In summer, vegetation is generally abundant in forests as well, while during winter snow cover may prevent the red deer from utilizing pastures to a large extent. The functional response was less apparent in summer than in the remaining seasons; during spring the functional response was strongest. This is probably a consequence of the different distribution of forage and cover through the seasons. However, the seasonal pattern in the functional response differed in the two regions. In contrast to Sunnfjord, the functional response was strongest in summer and weakest during winter in the Nordfjord region. Within home ranges in Nordfjord, there was 15.5% more forest of high productivity than in Sunnfjord, and 12% less marshland and mountains, whereas the distribution of the other habitat types was approximately equal. Thus, we may speculate that an interaction between seasonality and landscape architecture could be affecting these trade-offs.

In elk, highly nutritious forage on meadows was traded for lower quality forage in forests during the hunting season (Morgantini and Hudson 1985). Whether individuals taking a higher risk as the availability of pastures increases in the landscape actually grow more, at the risk of being predated, remains to be determined. Indeed, relating multiple-habitat-type use to fitness traits is possible and clearly a goal, but obtaining such data is extremely difficult and has so far only been done for the island population on Rum, Scotland (McLoughlin et al. 2006).

Concluding remarks

In many areas of the western world, deer populations have been expanding and increasing greatly in density in recent decades, causing concern regarding damage to agricultural crops, forestry, and biodiversity in their natural habitats (McShea et al. 1997, Gordon et al. 2004). The strong shifts in trade-offs linked to habitat selection shown here, driven by landscape-level variation in habitat compositions, will change the spatial distribution of grazing pressure, and therefore the resulting pressure on pastures relative to their natural habitat. Our study, in addition to yielding novel insight into deer behavior, thus also has the potential to enable more accurate predictions of damage to agricultural crops and threat to biodiversity as a function of landscape.

ACKNOWLEDGMENTS

This research was funded by the Research Council of Norway (AREAL-program and YFF-grant to A. Mysterud) and the Directorate for Nature Management. We are grateful to Knut Førde, Harald Kjær, and Odd Rønningen for help during fieldwork, and to Michael Angeloff for DEM-maps. We are grateful for helpful comments from Mark Hewison and Alain Licoppe on a previous draft.

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APPENDIX A

A detailed description of how GPS bias was corrected for and the minor effect this had on the results (*Ecological Archives* E090-049-A1).

APPENDIX B

Error ellipses for VHF data (*Ecological Archives* E090-049-A2).

APPENDIX C

Habitat classifications from digital resource maps provided by the Norwegian Forest and Landscape Institute (*Ecological Archives* E090-049-A3).

APPENDIX D

Plots showing use of pastures for 62 female red deer in Norway in relation to availability (*Ecological Archives* E090-049-A4).

Appendices – Paper I

Appendix A

Correcting for potential GPS bias

An overview of all GPS-collars used on red deer including success rates are given in table A1.

To model the probability of acquiring a GPS fix, stationary GPS collars were placed in the study area. We used 9 Televilt Tellus Basic GPS collars, 6 store-on-board and 3 GSM collars (2004-2005 production; Televilt TVP Positioning AB, Lindesberg, Sweden; the same type as used on the red deer). Trials were conducted in Jølster municipality in Sunnfjord, Sogn og Fjordane, during early October 2007. The collars were placed in every combination of habitat (open = pasture; closed = forest), slope (flat <10º, moderate = 10-20º, steep >20º) and aspect (north = 315-45º, south = 135-225º), and trials were repeated 4-6 times for each combination. Suitable locations had to be homogenous for habitat, aspect and slope in a radius of 40 m. The exact location for the collar was randomized by drawing a number between 0-360, and walking 20 steps in the corresponding compass direction. The collars were placed 1 m above the ground with the antenna directly upright, and left for ≥ 22 h. The collars were programmed with the same time intervals used in GPS collars on the red deer.

Several characteristics of the trial site were measured in the field, including percentage open canopy, tree density, tree height, tree diameter and horizontal view. The percentage open canopy was measured using the average spherical concave densiometer estimate across 4 readings, one in each of the 4 cardinal directions (Lemmon 1956, 1957). Tree density, height and diameter at breast height were recorded within a 10 m radius of the collar. Horizontal view was measured in a random compass direction drawn from a list of numbers ranging from 0-360. The remaining terrain variables were derived from Geographic Information System (GIS) by means of a 20 m digital elevation model with a 25 m cell size, using ArcView GIS 3.3 and ArcMap (ESRI, USA). Terrain indices included slope, aspect and altitude at the test site, and percentage visible sky, defined as the amount of a hemispherical dome centred over the location, that was not obstructed by terrain. The percentage visible sky was calculated using a sky visibility script in ArcView GIS 3.3 (developed by David O. Wallin, Department of Environmental Science, Huxley College of Environment, Western Washington University).

Accounting for habitat specific bias in GPS success rate

Of the nine stationary collars used to estimate fix success in various habitats, one collar failed to obtain locations. The eight remaining GPS collars successfully acquired locations at each of 62 testing sites. Fix success rate of the stationary collars averaged 97.6%, ranging from 77% to 100% at the individual sites. The average fix success rate was 99.4% on pastures and 96.8% in forested habitats.

We initially ran univariate logistic regression models with success or failure of obtaining a fix as response variable, and correlation tests for all variables that could have an influence on fix success. The univariate logistic regression models indicated that habitat, percentage open canopy, tree height and diameter at breast height, horizontal view, sky visibility, altitude and collar id all had an influence on the probability of fix success in the stationary GPS collars (Table A2). All significant parameter estimates of habitat variables observed in the field were correlated (Pearson $r > 0.5$) with variables derived from the GIS. We proceeded with multivariate analyses including only GIS variables as these could also be derived from all pixels in the entire study area.

We ran a stepwise AIC model selection (function stepAIC in library MASS [Venables and Ripley 2002], implemented in the statistical software R [R Development Core Team 2010]) starting with a logistic regression model with success or failure of obtaining a fix as response variable, and habitat, sky visibility, altitude, aspect, slope and GPS collar, and the interactions between habitat and slope, and habitat and sky visibility, as predictor variables. The most parsimonious model (lowest AIC) included habitat, sky visibility and GPS collar as predictor variables. GPS collar probably remained a covariate in the most parsimonious model because one of the collars showed a fix rate considerably lower than the rest (80.3%; the remaining seven collars 97.9-100%). To accommodate random variation in fix rate between collars, we fitted a logistic regression model with random intercepts for each GPS collar (Wood 2006: 310-315). GPS fix success rate was thus modeled by the equation

$$P_{success} = \frac{\exp(\beta_0 + \beta_1 x_{1ij} + \beta_2 x_{2ij} + \gamma_{0j})}{1 + \exp(\beta_0 + \beta_1 x_{1ij} + \beta_2 x_{2ij} + \gamma_{0j})} \qquad \text{eqn 1}$$

where observations $i = 1\ldots n$ are clustered within strata $j = 1\ldots m$, i.e. locations in GPS collars. $P_{success}$ is the probability of successfully acquiring a GPS location, β_0 is the mean intercept, β_1 and β_2 are the fixed effect coefficient estimates for the covariates habitat (x_1) and sky visibility (x_2), and γ_{0j} is the random intercept, which is the difference between the mean intercept β_0 for all groups, and the intercept for group j (Skrondal and Rabe-Hesketh 2004). Models with random effects were formed using the library lme4 (Bates et al. 2012) implemented in R. Eqn 1 predicted lower probability of acquiring a fix in forested habitats than on pastures, and showed a tendency of an increasing probability of fix success with increasing sky visibility (Table A3). The fixed effects parameter estimates from the model were used to make a map of the probability of obtaining a GPS fix in each pixel of the study area, using the raster calculator in ArcMAP.

We used iterative simulation to correct for possible GPS bias in the red deer GPS data prior to analyzing habitat selection (Frair et al. 2004). For each missing location (or deleted outlier), we randomly selected a location within a rectangle defined by the last and next known location. Thereafter a random number between 0 and 1 was drawn. If the random number was above the predicted value of acquiring a fix for that pixel (found from the probability map), the location was retained. If the random number was below the probability of getting a fix, a new random location was selected. In this way, locations with the lowest predicted probability of acquiring a fix, and thus higher probability of being a missing location, was retained.

Results from the modeling of corrected and uncorrected data show a very high degree of qualitative consistency, but with some change in exact estimate (Fig. A1 & A2).

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Table A1. Information on the 40 GPS collared female red deer in Sunnfjord, Norway used in the analyses. Individual and overall success rates of GPS collars are given as successful fixes divided by attempted fixes. SOB = Store-on-board, GSM = Global System for Mobile communications. All collars are Televilt Tellus collars (Televilt TVP Positioning AB, Lindesberg, Sweden).

Id	Tracking period		Collar type	Attempted	Success	Success rate
	Start	Stop				
142009_2005	2005-01-30	2006-01-13	Basic SOB	16583	15170	91
142021_2005	2005-01-22	2005-07-11	Basic SOB		Early mortality	
142034_2005	2005-01-30	2006-01-13	Basic SOB	16583	15371	93
142045_2005	2005-01-27	2006-01-13	Basic SOB	16636	14796	89
142074_2005	2005-01-24	2005-11-21	Basic SOB	14676	12975	88
142088_2005	2005-01-30	2005-10-06	Basic SOB	12053	9249	77
142119_2005	2005-01-30	2006-01-13	Basic SOB	14590	11598	79
142175_2005	2005-01-27	2005-11-19	Basic SOB	10700	9310	87
142205_2005	2005-01-24	2006-01-03	Basic SOB	16462	14707	89
142215_2005	2005-01-27	2005-12-02	Basic SOB	15672	12720	81
142224_2005	2005-01-30	2006-01-13	Basic SOB	16571	14353	87
142250_2005	2005-01-24	2005-12-13	Basic SOB	15769	14480	92
142259_2005	2005-01-27	2005-12-02	Basic SOB	15219	14080	93
142269_2005	2005-01-27	2005-12-16	Basic SOB	15765	14149	90
142280_2005	2005-02-19	2006-01-03	Basic SOB	15426	14799	96
142339_2005	2005-03-05	2005-12-08	Basic SOB	14042	12637	90
142350_2005	2005-03-07	2005-11-24	Basic SOB	13249	12810	97
142360_2005	2005-03-10	2005-12-13	Basic SOB	14040	13466	96
142385_2005	2005-03-05	2005-12-27	Basic SOB	14699	13908	95
142395_2005	2005-02-19	2005-12-21	Basic SOB	15057	13606	90
142422_2005	2005-03-05	2005-12-06	Basic SOB	13994	13354	95
142434_2005	2005-03-05	2005-12-06	Basic SOB	13995	12062	86
142445_2005	2005-03-05	2005-12-06	Basic SOB	13987	12886	92
142455_2005	2005-02-19	2005-11-24	Basic SOB	13824	12397	90
142009_2006	2006-03-21	2006-12-21	Basic SOB	13958	13038	93
142034_2006	2006-03-29	2006-11-17	Basic SOB	11868	11689	98
142074_2006	2006-03-09	2006-12-21	Basic SOB	14458	13391	93
142088_2006	2006-03-06	2006-11-14	Basic SOB	12781	11682	91
142175_2006	2006-03-30	2006-11-17	Basic SOB	11868	10127	85
142205_2006	2006-03-22	2006-11-14	Basic SOB	12419	10598	85

142215_2006	2006-03-02	2006-12-21	Basic SOB	14890	13174	88
142250_2006	2006-03-06	2006-11-14	Basic SOB	12780	11872	93
142259_2006	2006-04-05	2006-11-14	Basic SOB	11632	10861	93
142300_2006	2006-03-21	2007-01-17	Basic GSM	14819	13085	88
142350_2006	2006-03-01	2006-11-17	Basic SOB	12971	11949	92
142395_2006	2006-03-16	2006-11-17	Basic SOB	12399	11456	92
142422_2006	2006-03-09	2006-12-21	Basic SOB	14465	14013	97
142434_2006	2006-03-01	2006-11-17	Basic SOB	12971	12185	94
142445_2006	2006-03-09	2006-12-21	Basic SOB	14459	13762	95
142455_2006	2006-03-06	2006-11-14	Basic SOB	12782	12106	95
			Mean:	**14131**	**12817**	**91**

Table A2. Results from univariate logistic regression to predict the probability of fix success in stationary GPS collars, based on 8 GPS collars at 62 test sites in Jølster, Sogn og Fjordane.

Variable	**Variable range**	**Range in predicted $P_{success}$**	**Df**	**Deviance**	**Resid. Df**	**Resid. Dev**	**P(>|Chi|)**
Habitat [a]	0-1	0.95-1.00	1	30.17	1503	408.6	<0.001
Open canopy (%)	2.86-99.84	0.93-0.99	1	30.36	1.50E+03	408.41	<0.001
Tree density	0-170	0.94-0.97	1	1.44	1503	437.33	0.23
Horizontal view (m)	6-300	0.94-1.00	1	16.15	1503	422.63	<0.001
Tree height (m)	0.0-37.5	0.84-0.99	1	37.62	1.50E+03	401.16	<0.001
Tree diameter (d.b.h.)	0.00-29.04	0.84-0.99	1	47.74	1.50E+03	391.03	<0.001
Sky visibility (%)	63.31-80.24	0.93-0.98	1	4.64	1503	434.13	0.03
Altitude	81-561	0.94-0.99	1	4.91	1503	433.86	0.03
Aspect [b]	1-3	0.96-0.97	2	0.8	1.50E+03	437.98	0.67
Slope	0.0-30.2	0.95-0.98	1	1.51	1503	437.27	0.22
GPS collar [c]	1-8	0.80-1.00	7	117.99	1.52E+03	322.06	<0.001

[a] Habitat classes (0 = pastures, 1 = forests)

[b] Aspect classes (1 = flat, 2 = moderate, 3 = steep)

[c] GPS collar (Categorical variable from 1-8, each representing an individual GPS collar)

Table A3. Mixed-effects logistic regression model based on the highest-ranked logistic regression model for predicting the probability of a GPS collar successfully acquiring a fix, based on 8 GPS collars at 62 test sites in Norway. HPD intervals = highest posterior density intervals (Plummer et al. 2008). N_{obs} = 1505.

Random effects		**HPD intervals**	
Variable	**SD**	**Lower**	**Upper**
GPS collar	1.3167	0.658	9.590

Fixed effects			**HPD intervals**	
Variable	**β**	**SE**	**Lower**	**Upper**
Intercept	2.630	2.742	-2.742	7.983
Habitat [a]				
Forest	-2.449	1.046	-5.618	-0.649
Sky visibility	0.053	0.033	-0.006	0.118

[a] Reference = pastures

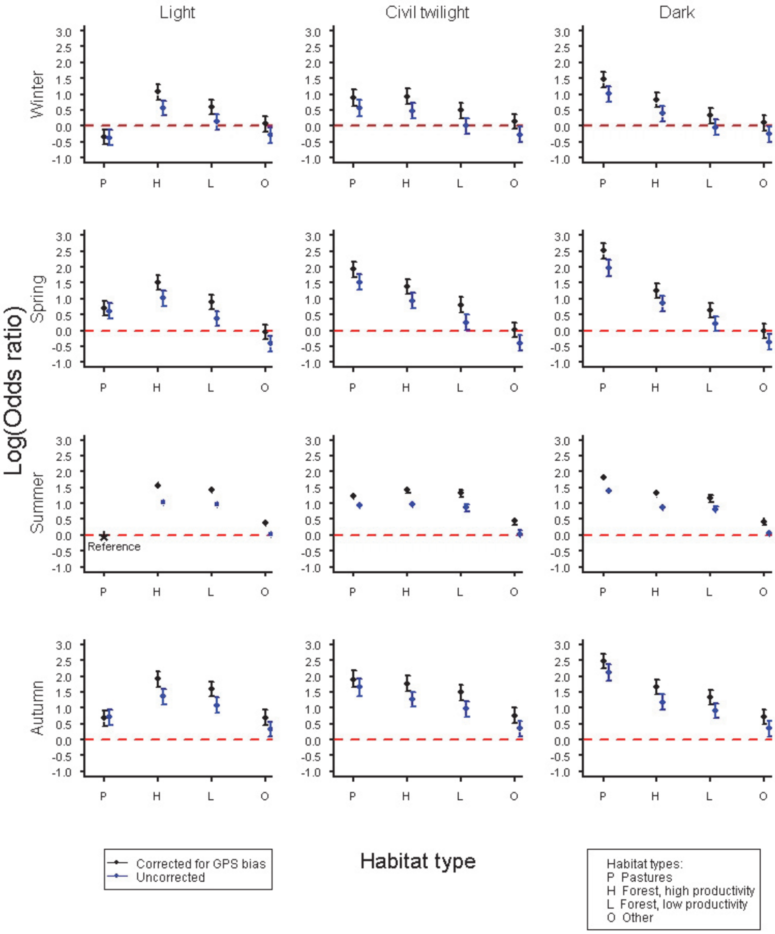

Figure A1. Comparing habitat selection through different seasons and light intensities for a data set corrected for potential GPS bias induced by missing locations (black), and an uncorrected data set (blue). The data sets contain GPS locations from 40 female red deer in Sunnfjord, Norway. Estimates are log odds ratios ± 95% highest posterior density intervals, where the log odds ratios are calculated relative to selection of pastures in summer during daylight (asterisk). The red line specifies the reference level, and values above 0 indicate higher selection of the particular habitat type relative to the reference, while values below 0 indicate lower selection. The letters P-H-L-O on the x-axis specifies the different habitat types (provided in the legend).

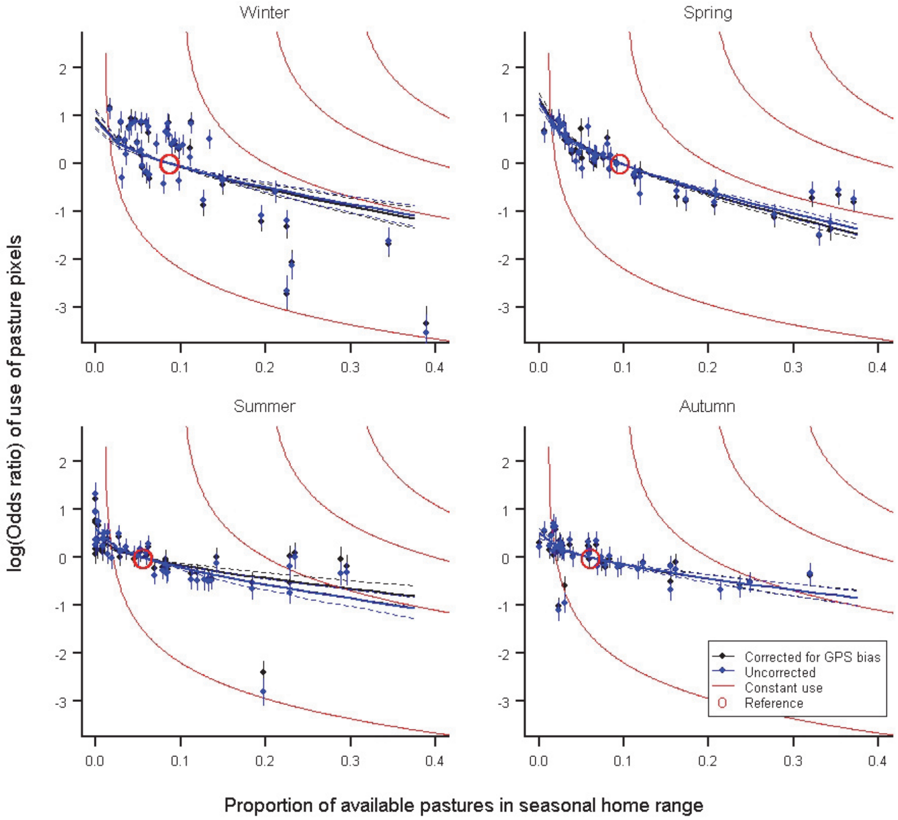

Figure A2. Comparing functional responses in the selection of pastures for a data set corrected for potential GPS bias induced by missing locations (black), and an uncorrected data set (blue). The data sets contain GPS locations from 40 female red deer in Sunnfjord, Norway. The log odds ratios of the use of pasture pixels are calculated relative to average available pastures in the seasonal home range (red circles), and is a measure of selection. The points are individual red deer, and the dotted lines represent 95% highest posterior density intervals. Red lines illustrate constant use of pastures.

Appendix B

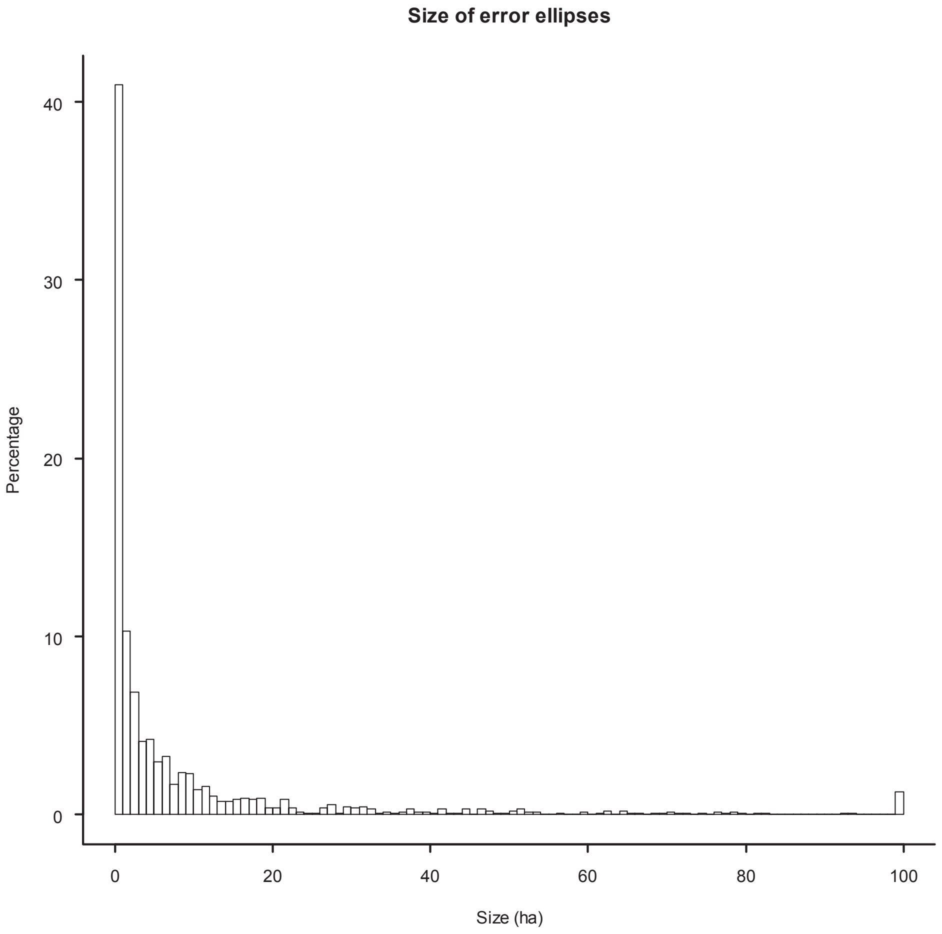

Figure B1. Distribution of the size of error ellipses for 22 VHF collared female red deer in Norway, in ha. All error ellipses larger than 100 ha (n = 17) have been set to the size 100 ha. As the size was generally low (mean = 10.65 ± 1.95 ha, median = 1.85 ha, range 0.00 - 675.66 ha), all locations were included in the analyses.

Appendix C

Table C1. Habitat classifications from digital resource maps provided by the Norwegian Forest and Landscape Institute. The habitat types used in the analysis are obtained from merging of selected habitat types in the original maps.

	Habitat types	**Description**
1	Pastures	Agricultural land cultivated at various degrees [a], and pastures
2	Forest, high productivity	Forested habitats with high productivity [b]
3	Forest, low productivity	Forested habitats with normal to low productivity, and unproductive forests [b]
4	Other; Marshland, mountains and bare rock	Marshland, areas not previously classified, bare rock and selected uncharted areas [c]
5	Lakes, fiords and uncharted areas [d]	Any permanent flowing or non-flowing water and other uncharted areas (very few)

[a] 90% grass (Yngve Rekdal, the Norwegian Forest and Landscape Institute, pers. comm.)

[b] Forest types are classified after the area's wood-producing potential. There is no information on the species composition.

[c] Uncharted areas consists primarily of barren mountains at high elevations (Rolf Bekkhus, the Norwegian Forest and Landscape Institute, pers. comm.). This habitat type is likely of little importance as deer habitat. However, some cells may contain productive areas as well. This will be an unknown (but likely minor) source of error in our analyses.

[d] Removed from the analysis

Appendix D

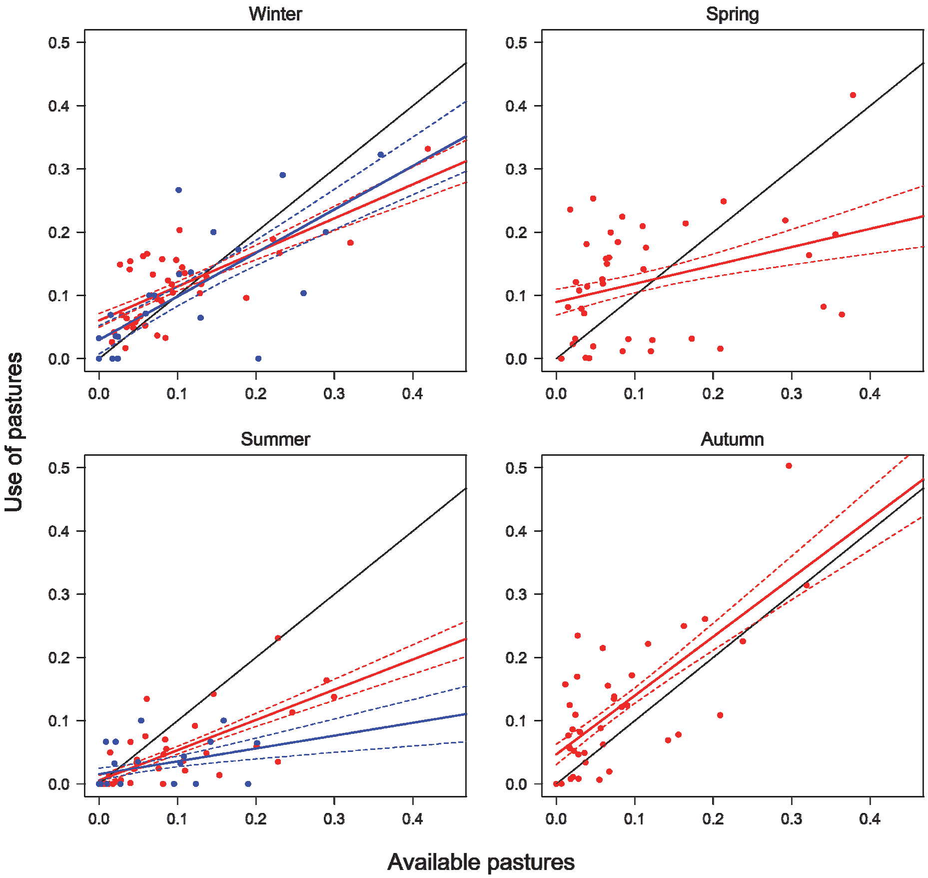

Figure D1. Plots showing use of pastures for 62 female red deer in Norway (Sunnfjord/GPS: red; Nordfjord/VHF: blue) in relation to availability. The x-axis shows proportions of available pastures within seasonal home ranges, and the y-axis shows proportion of use of pastures. The points are individual red deer. The black line illustrates use proportional to availability (ß = 1), and the colored lines show actual use in relation to availability by the red deer. The dotted lines represent 95% confidence limits.

II

III