Habitat selection in red deer (*Cervus elaphus*) at the within home range scale

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Preface

This study was conducted at the University of Oslo, Norway, under the supervision of Atle Mysterud, Leif Egil Loe and Vebjørn Veiberg. I would like to thank my supervisors for great help and guidance during the past two years. Thank you for always being available and answering my numerous questions. Many thanks go to Atle Mysterud for giving me the chance to experience the fieldwork and write this master thesis. Thank you for your quick responses, always giving me the drive to move forward. Leif Egil Loe deserves special thanks for guiding me through the process of analyses, and Vebjørn Veiberg for sharing all his knowledge of Sogn og Fjordane and the red deer populations with me.

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I thank my family for always being supportive, and helping me in every way. Last but not least, I sincerely thank my fiancé Birger Godvik for constantly being there for me. You keep my spirits up, and always give me something to look forward to.

Inger Maren,
Blindern, August 30th 2007.

Abstract

The red deer (*Cervus elaphus*) are among the most important game species in Norway, with a tenfold increase in harvest over the last few decades. Despite its importance, information regarding red deer habitat selection is limited. In this study, year-round habitat selection at the within home range scale was investigated using data from female red deer equipped with either VHF- or GPS-collars in the county of Sogn og Fjordane. I predicted that red deer habitat selection would be determined by spatial and seasonal fluctuations in forage quality and quantity, such that the habitats holding the most nutritious forage would be selected through the year. I also predicted that the red deer would experience a trade-off between forage availability and safety, leading to more covered habitats being selected in daytime when visibility is good, and open habitats being selected at night-time. Habitat selection was investigated using resource selection functions, separated by season and time of day/state of activity to determine the underlying mechanisms. Red deer habitat selection changed through the seasons as would be expected if forage quality and quantity fluctuated through the year, and varied between habitats. Cultivated habitats were frequently selected by the red deer, and as these habitats are regarded to hold forage of relatively higher nutritional value than forage occurring naturally through most of the year, I argue that agricultural land and pastures are very important to the red deer. Habitat selection also changed with time of day/state of activity, suggesting a trade-off in habitat selection. Further evidence for a trade-off situation was found in the use of agricultural land and pastures, as the red deer select for these habitat types when availability is low, and use them less than expected when they are more readily available. Staying away from open, exposed areas when visibility is good should lower the chance of being detected, and therefore increase survival. This study of red deer habitat selection reminds us that habitat selection is a dynamic process. Resource selection functions are powerful tools to characterize habitat selection, and by extending the analyses by taking relevant temporal scales into account, the mechanisms behind habitat selection can be identified.

Contents

1 Introduction

Animal habitat selection is an important component of the ecology of a species (Rosenzweig, 1981). Finding out how animals use the resources available to them provides information about requirements for reproduction and survival. Solid information about how the animals use their habitat is therefore central to drawing conclusions in management and how to preserve endangered species. Habitat selection is defined as disproportionate use of some habitats relative to others (Johnson, 1980). When animals choose a habitat, they often have to consider many factors, such as forage quality and availability, shelter and potential predators. Each habitat type may not always contain an adequate mixture of these factors. The resulting choice of habitat is thus the outcome of trade-offs between the costs and benefits the habitat holds (Lima & Dill, 1990; Mysterud & Ims, 1998). One such trade-off may take place when exposed habitats provide the best forage, while closed habitats provide shelter against harsh weather and 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 & McCullough, 1990; Manly *et al.*, 2002). For example, animals may spend their active foraging time in more risky habitats where forage is abundant, and rest in safer retreat habitats with less available forage (Mysterud *et al.*, 1999a).

Analyses of habitat selection are generally conducted by comparing the habitat types used to what is available to the animals. The definition of what is available is often a question regarding at what spatial scale a given choice is taken. Habitat selection occurs in a hierarchical fashion (Senft *et al.*, 1987), often classified into four orders of selection (Johnson, 1980), ranging from the geographical range of the species, through the home range and the various habitats patches within the home range, and finally to the use of different food items within the habitat patch. 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, I therefore focus on the within home range scale. One of numerous methods available for investigating habitat selection is resource selection functions (RSFs). RSFs are defined as any function proportional to the probability of use of a resource unit or area by an animal (Manly *et al.*, 2002). This method have been applied for studies on habitat selection across a diverse range of species, from pileated woodpeckers (*Dryocopus pileatus*) (Lemaitre & Villard, 2005) to moose (*Alces alces*) (Osko *et al.*, 2004) and grizzly bears (*Ursus arctos*) (Nielsen *et al.*, 2002). When addressing relationships between the environment and species inhabiting it, models like RSFs are powerful tools, and have become increasingly common in ecology. RSFs can be calculated when the distribution of resources are known within an animal's home range, and locations for resource use by the individual are identified. The RSFs are averages over the period the data are collected, and generally the selection times should be kept as short as possible as the habitats may change (Manly *et al.*, 2002), e.g. between season. When analyzing data from a seasonal environment, it is important to at least separate the analysis between the main seasons with largely varying conditions.

There are situations where the estimation of RSFs could be less informative. This could be the case if there are trade-offs between several factors affecting habitat use as described above. In such trade-off situations, the selection of a resource differs contingent on the availability of that resource (Mysterud & Ims, 1998; Gillies *et al.*, 2006). A rare resource item can be highly favored, but utilization might be inhibited due to its rare occurrence. If a less favored resource is the only one available, it will be utilized more out of necessity (Manly *et al.*, 2002). Selection for the various habitat types may therefore be conditional on availability. This means that we might not be able to see how important the particular resource is to the animal simply by looking at the relative use (Mysterud & Ims, 1998; Gillies *et al.*, 2006). Mysterud & Ims (1998) defined this change in relative use of habitat types with changing availability as a functional response in habitat selection. For ruminants, these trade-offs often arise since animals select different habitats when resting/ruminating and foraging, and during day and night. Foraging often takes place in open habitats where forage is abundant, while rumination and rest is carried out in more covered habitats with less forage. It is also common to use more open forage-rich habitats in night-time, and covered habitats with less forage during daytime (Mysterud & Ims, 1998; Mysterud *et al.*, 1999a). Surprisingly few habitat selection studies have taken these insights into account by either separating the analysis on time of day (day vs. night) or state of activity (resting vs. foraging), and only one study on moose have actually measured whether this gives rise to functional responses in habitat selection (Osko *et al.*, 2004).

The red deer (*Cervus elaphus*) are among the most important game species in Norway. With a tenfold increase in harvest the last few decades, a harvest of 29200 red deer was reached in 2006 (Statistics Norway, 2006). The life history and the demography of the Norwegian red deer have been studied extensively (e.g. Langvatn *et al.*, 1996; Loison & Langvatn, 1998; Mysterud *et al.*, 2001; Langvatn *et al.*, 2004). Despite its importance, information regarding red deer habitat selection in Norway is limited. Habitat selection by red deer was studied in central and western parts of Norway in the 1960s and -70s (Ahlén, 1965), but mainly by snow tracking, and focusing on diet on a very fine spatial scale. In the county of Sør-Trøndelag, coarse scale migration pattern have been studied (Albon & Langvatn, 1992). However, no extensive studies of within home range selection have been conducted based on marked individuals. In this study, I investigate habitat selection in individually marked red deer (VHF- and GPS-collars) in the county of Sogn og Fjordane (Fig. 1), which has the highest number of harvested red deer in Norway. I provide the first detailed account of seasonal variation in selection of forest types, agricultural pastures, and other available habitat types at the within home range scale. A more specific aim of the study was to test hypothesis and quantify possible trade-offs in habitat selection through the various seasons as detailed above.

There is no detailed information available regarding the amount of forage and shelter in the various habitat types. However, agricultural land and pastures are widespread and regarded important to red deer. These habitat types offer generally abundant forage and little canopy cover, providing an opportunity to address the topic properly. If there are trade-offs, I predict a higher selection for agricultural land and pastures during night (when foraging) than during day (when resting). Further, due to differential availability of agricultural land and pastures, I predict an overall functional response in habitat selection, i.e., that selection is dependent on availability. It has also recently been suggested that GPS data may be used to evaluate habitat quality, by looking at speed of movement (Morales *et al.*, 2004). I predict that the fastest movement between two locations will be in more covered habitats, due to lower risk of detection. I also predict that they will move faster in months where forage is abundant and of high energetic quality (see Table 1 for an overview of numbered hypotheses with corresponding predictions).

Table 1. An overview of hypotheses (H) and corresponding predictions (a-c) investigated.

Hypotheses and predictions

H1. Habitat selection is determined by spatial and seasonal fluctuations in forage quality and quantity.

  a. Habitats of high productivity (likely holding high quality and quantity of forage) will be more frequently selected in all seasons.
  b. Assuming the difference in forage quality in forests and pastures is larger during winter than in summer, I expect use and selection of pastures to be higher in winter.
  c. Movement will be faster in seasons with higher forage quality, as animals spend less time ruminating.

H2. Habitat selection is determined by a trade-off between forage availability and safety.

  a. Habitats with more cover (forests) will be more frequently selected in daytime/inactive state, at the expense of forage quantity and quality (agricultural areas).
  b. There will be functional responses in habitat selection between individuals, i.e., that selection of open habitats rich in forage will be contingent on availability.
  c. Movement will be faster in covered habitats due to lower risk of detection.

2 Materials and methods

2.1 Study areas

The study area is located in the western part of southern Norway, and consists of 3 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 and pine forest (*Pinus silvestris*), 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, 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, while snow depth and duration of snow cover increases (Langvatn *et al.*, 1996). Snow cover is normally present at the coast in January and February, but highly variable among years. Mean temperature was 0.3 °C in winter and 16.2 °C in summer 2006, and mean precipitation was 24.4 mm and 22.5 mm for winter and summer respectively (see Appendix 3, Table A2 for a classification of the seasons).

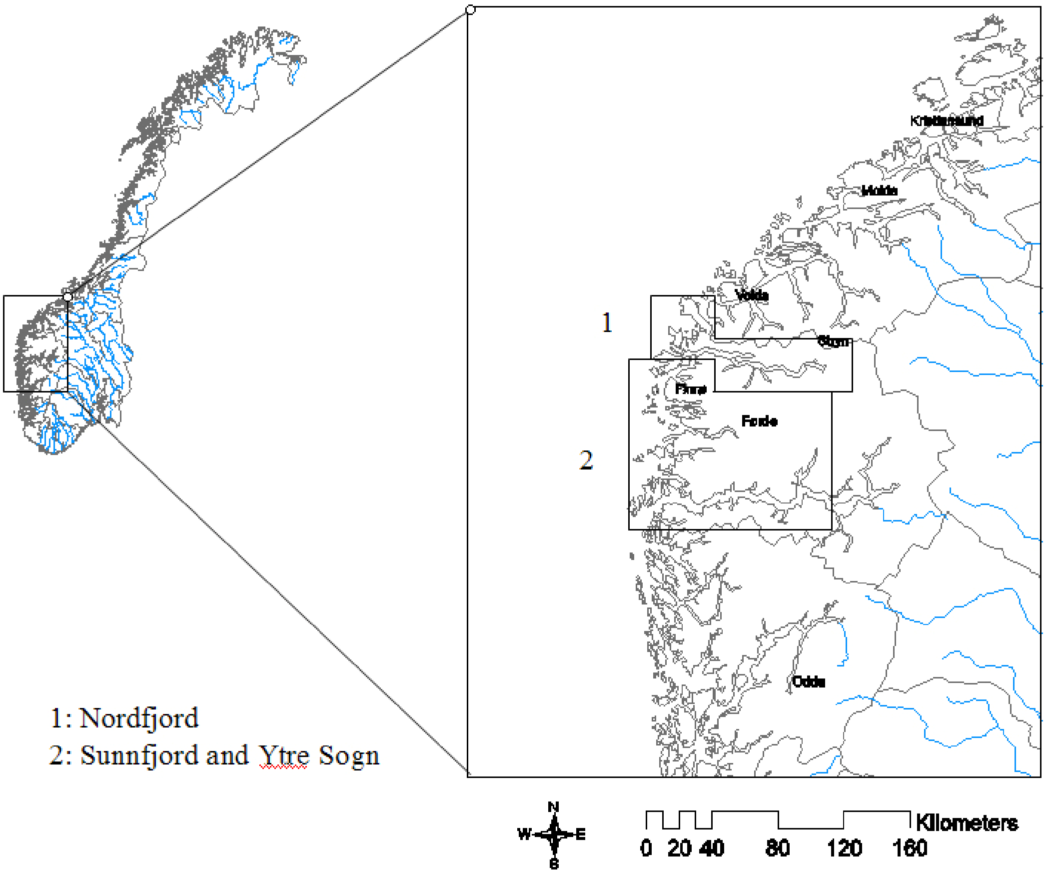

Figure 1. Map of the study area situated in the western part of Southern Norway. Boxes represent the different regions inhabited by the red deer in this study.

2.2 Red deer data

2.2.1 Nordfjord area - VHF collared deer

Between 2001 and 2005, 104 female red deer were caught on winter feeding sites in Nordfjord. The animals were fitted with VHF collars as well as colored and numbered ear tags to record location and activity through the year. Of the available 57 marked deer with functional collars in 2006, 22 female red deer were selected for this study based on the limitation that it should be possible for two persons to track all of them within a day. These deer were subsequently tracked using Televilt and Telonics tracking equipment once a day during two periods in winter (15.02.06 - 01.03.06 and 15.03.06 - 31.03.06) and two periods in summer (13.06.06 - 07.07.06 and 31.07.06 - 07.08.06). At least three bearings were taken from different observer positions for every individual to obtain a more precise position. I aimed for shortest possible time between each bearing, and the difference between the angles should be >20º. If I obtained visual observations of individuals, the position was located with a GPS. A total of 60 positions were obtained for each individual, 30 each season. Activity was determined by sensors in the collars, based on different pulse rates (0.6 second pulse rate when active and 1.2 seconds when inactive). Most of the radio-tracking were 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. One third of the positions were obtained during night-time (defined as after darkness).

2.2.2 Sunnfjord and Ytre Sogn area - GPS collared deer

In the area of Sunnfjord and Ytre Sogn (hereafter termed Sunnfjord for convenience), 25 female red deer were caught (using the same method as above) and fitted with Televilt GPS collars in January and February 2005 and another 20 females in March 2006. Of these, 23 of the collars from 2005 and 8 from 2006 were retrieved by the onset of my analysis. The collars were programmed to record a position once every hour, and every two weeks a positions were recorded in six minute intervals for a 24 hour period. After approximately 10 months a drop-off mechanism released the collars, and they were collected to download the data for analysis. There were no activity switches in these collars.

2.3 Statistical analysis

2.3.1 Initial formatting and screening of data

Data from red deer fitted with VHF collars were processed in LOAS 4.0b (Ecological Software Solutions, USA). I estimated individual locations together with associated error ellipses, using standard triangulation techniques (White & 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 low, and all locations were included in the analysis (see Appendix 1, Fig. A1).

The data from the GPS-collared red deer were downloaded to excel for cleaning and analyses. In the cleaning, all locations taken before date of marking and on the first day of marking were deleted. As disregarding 2-D data and data with low geometrical strength of the GPS satellite configurations (expressed as high positional dilution of precision (PDOP)) would result in loss of a lot of possibly informative data and maybe introduce biases (D'Eon & Delparte, 2005), only outliers were removed. All positions where the animals had moved more than 10 km per hour were inspected (typically less than 0.1% of locations). The majority of these locations were large GPS errors that could be removed based on impossible speed (on the order of several hundred km per hour). Remaining locations (with realistic speed level) were removed if they occurred a) in water or b) on the other side of a fiord, and only if the next location was in close proximity to the previous location. As this study analyses selection at the within home range scale, the deletion of outliers are regarded of no influence on results. GPS success rate is given in Appendix 2, Table A1.

2.3.2 Habitat types

Vegetation types (defined as habitat types in my study) were derived from digital land resource maps provided by the Norwegian Forest and Landscape Institute (NIJOS), with scale 1:5000. The digital resource maps were divided into 13 habitat types; 1-4) Agricultural land cultivated with varying intensities, 5) pastures, 6) forest, very high productivity, 7) forest, high productivity, 8) forest, medium productivity, 9) forest, low productivity, 10) forest, other, 11) marshland, 12) other areas with more than 30 cm soil depth 13) other areas with less than 30 cm soil depth and bare rock. A layer of water was added to distinguish mountains from lakes and ocean. This new layer formed 4 new habitat types; 14) uncharted areas; this consists primarily of barren mountains at high elevations (Rolf Bekkhus, NIJOS, 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; 15) ocean, 16) lakes 17) other uncharted areas (very few). The original habitat types were then reduced to 8 in the final version of the maps: 1) agricultural land (90% grass; Yngve Rekdal, NIJOS, pers. comm.; from habitat type 1, 2 and 3 in the original maps), 2) pastures (4 and 5), 3) forests, very high productivity (6), 4) forests, high productivity (7), 5) forests, medium to low productivity (8, 9 and 10), 6) marshland (11), 7) mountains and bare rock (12, 13 and 14) and 8) lakes, fiords and uncharted areas (15, 16 and 17). The final versions of the maps were rasterized in ArcMAP (ESRI, USA) with a resolution of 50m x 50m. The raster maps were converted to ASCII for use in the analyses.

2.3.3 Resource selection functions

Resource selection functions (RSFs) were estimated to examine the deer's selection of habitats. RSFs compute the ratio between used and available habitat, termed the selection ratio (Manly *et al.*, 2002). I used a design based on used and available habitat types at the level of each individual, so-called design III data (Boyce *et al.*, 2002; Manly *et al.*, 2002). I fitted RSFs by using the function widesIII in the package adehabitat (Calenge, 2006), implemented in the statistical software R (R Development Core Team, 2006). The widesIII function computes the selection ratios for design III data. I used hourly positions for the GPS collared individuals, and ran separate analyses for each season (see Appendix 3, Table A2), and time of day (day: 6:00 – 22:59/night: 23:00 – 5:59). For the VHF collared individuals separate analyses were run on daily positions for each season and state of activity (inactive/active; state of activity was not available for GPS-collared deer).

Availability. The habitat availability for the individual animals corresponded to the proportion of pixels in each available habitat type in their 100% Minimum Convex Polygon (MCP) full year home ranges. For each individual, the estimates of availability are therefore the same for all seasons and time of day/state of activity.

Use. Habitat use is the number of positions for each individual in each habitat type. In contrast to availability I calculated use for each combination of season and activity type/time of day. Availability and use of habitat type 8 (lakes, sea and uncharted areas) were eliminated from the analysis.

Chi-square tests of habitat selection were run both at the population level and at the individual level. The mean selection ratios (population level) and corresponding 95% confidence limits were plotted for each season, region and time of day (GPS-collars) or state of activity (VHF-collars). Selection ratios above 1 indicate selection of the particular habitat type, while values below 1 indicate avoidance. Confidence intervals not including 1 indicate significant selection or avoidance of the various habitat types. I was specifically interested in the use of agricultural land and pastures (habitat type 1 and 2), and therefore used the individual level selection ratios to calculate several descriptive statistics, such as the proportion of individuals using (ratio >0) and selecting (ratio>1) agricultural pastures.

Initially, I also performed an eigenvalue analysis (Calenge & Dufour, 2006) of the individual selection ratios. Eigenvalue analyses are extensions of principal component analysis (PCA), and investigate the variation of selection ratios for the individuals in the analysis. These analyses are mainly useful for initial screening of habitat types, and I therefore do not present the results.

2.3.4 Functional response in habitat selection

In a situation with only two habitat types, the use of logistic regression for assessing functional responses has been recommended (Mysterud & Ims, 1998). As this model did not fit the data well, likely due to the higher number of habitat types, I used a simple linear model (LM) to determine if there were trade-off situations by regressing use on availability of agricultural land and pastures. LMs were run separately for GPS- and VHF-collared individuals for each season. The regression slope (β) of the equation gives information about potential functional responses in habitat selection (Mysterud & Ims, 1998). A slope of one ($\beta = 1$) implies that use is proportional to the habitat availability, and thus no functional response. When the slope is zero ($\beta = 0$), all individuals spend a consistent amount of time in each habitat, regardless of availability. Slopes between 0 and 1 indicate functional responses in habitat selection.

2.3.5 Speed

Only the GPS-collared red deer were used when analyzing speed of movement. In addition, only positions with 6 minutes time interval were used since these will represent true speed more closely than positions taken with hourly or daily time intervals.

When analyzing the effect of habitat on speed, I used only the positions were the red deer did not change habitat types between two consecutive positions. For each season, I calculated the mean of the speed per habitat type for each individual, and counted the number of observations per individual per habitat type. From these values, population level weighted mean speed and 95% confidence limits were calculated and plotted for each season and habitat type. The weighted means were plotted with the size of the points reflecting the amount of positions in each habitat type. Speed is obviously different when resting and when active, and some habitat types can be used more often for resting than others. Mean speed values will be sensitive to the proportion of resting fixes. To check for this, speed between two consecutive positions were plotted as a histogram to look for multiple peaks (a peak close to zero would likely represent resting periods and a peak at a higher value represent active periods).

When analyzing seasonal variation in speed, I calculated speed per month for each individual (again using only positions with 6 minute intervals). These values were used to calculate the weighted mean and the variance for speed each month at the population level. The data were then plotted with the weighted mean speed month and bars representing 95% confidence limits. The mean speed per month for each individual was also added to the plot as point estimates.

3 Results

3.1 Habitat selection

Red deer showed a very similar pattern of selection during winter, spring and autumn (Fig. 2). The main pattern was higher selection for agricultural land and pastures (habitat type 1 and 2) in night-time/active state (hereafter referred to as night-time) and avoidance of these habitat types in daytime/inactive state (hereafter referred to as daytime). In winter, red deer also selected for pastures in daytime. Forests of very high and high productivity (habitat type 3 and 4) were generally selected in daytime, but not as much in night-time. There was in general no particular selection or avoidance of forests of normal to low productivity (habitat type 5) during these seasons, and the red deer showed tendencies towards avoidance of marshland and mountains and bare rocks (habitat type 6 and 7). Confirming hypothesis H1a and H1b, summer differed from the three other seasons by overall lower selection of agricultural land and pastures, and a higher selection of all three forest types.

As predicted from hypothesis H2a, the deer showed a tendency of overall higher selection for agricultural land and pastures (habitat type 1 and 2) during night-time than in daytime, when these habitat types mostly were avoided (Fig. 2). Selection for forest types was consequently higher in the daytime, when there mainly were higher levels of selection for forests of very high and high productivity, than in night-time. In daytime, deer selected forests to a higher extent than agricultural land and pastures. In night-time particularly agricultural land, and in winter also pastures, were generally more selected than the various forest types. There were no particular differences between day and night or state of activity for forests of normal to low productivity, marshland, or mountains and bare rock (habitat type 5, 6 and 7).

The overall selection pattern of red deer in Nordfjord and Sunnfjord was very similar (Fig. 2).

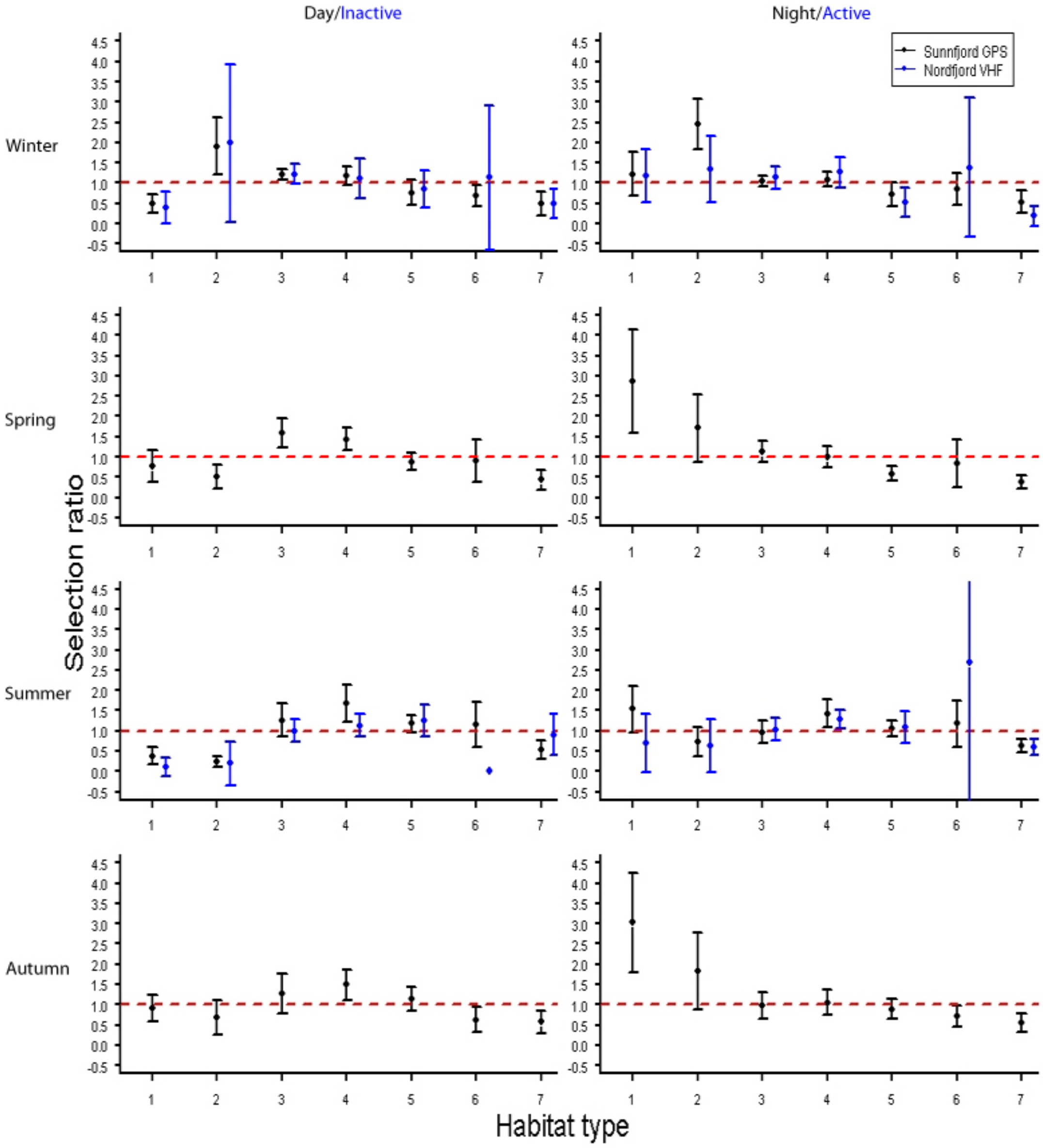

Figure 2. Comparing habitat selection through different seasons, and time of day for 31 GPS-collared red deer in Sunnfjord and state of activity for 22 VHF collared red deer in Nordfjord. Estimates are mean selection ratio ± 95% confidence limits. GPS-collared individuals are shown in black and VHF-collared individuals in blue. Values above 1 indicate selection of the particular habitat type, while values below 1 indicate avoidance. Numbers 1-7 specify the different habitat types; 1 = agricultural land, 2 = pastures, 3 = forests, very high productivity, 4 = forests, high productivity, 5 = forests, normal to low productivity, 6 = marshland and 7 = mountains and bare rock.

3.2 Agricultural land, pastures and functional responses in selection

The proportion of red deer that were recorded on agricultural land or pastures at some point was generally high (>64%). Those that were not recorded on agricultural land or pastures were mainly individuals in Nordfjord that did not include these habitat types in their home range (Table 2). Nearly all the GPS-individuals (with more frequent sampling of positions) used farmland. The majority of individuals selected farmland, regardless of region, season or time of day (except Sunnfjord at daytime in summer; Table 2). Proportions of use and selection were very similar in spring, autumn and winter. In summer, the proportion of deer selecting for agricultural land and pastures was lower (26%) than for the remaining seasons.

Table 2. Proportion of GPS-collared red deer in Sunnfjord and VHF-collared red deer in Nordfjord using, selecting or without access to agricultural land and pastures through the seasons. “Use” shows the proportion of individuals using habitat type 1 or 2 at some point (habitat type 1>0 or habitat type 2>0). “Selection” shows the proportion of individuals selecting habitat type 1 or 2 (habitat type 1>1 or habitat type 2>1). Both use and selection is calculated only based on the individuals that have habitat type 1 and 2 accessible within their home range. “NA” shows the proportion of individuals without access to habitat type 1 and 2 within their home range.

	Sunnfjord		**Nordfjord**	**Sunnfjord**		**Nordfjord**
	Spring	Summer	Summer	Autumn	Winter	Winter
Day						
Use	0.97	0.94	0.64	0.94	1.00	0.64
Selection	0.50	0.26	0.60	0.52	0.66	0.59
NA	0.03	0.16	0.60	0.03	0.06	0.32
Night						
Use	1.00	0.90	0.82	0.97	1.0	0.91
Selection	0.81	0.71	0.77	0.74	0.75	0.77
NA	0.06	0.10	0.55	0.03	0.09	0.32

The red deer selected agricultural land and pastures differently contingent on the availability, as predicted by hypothesis H2b (Fig. 3; Table 3). During both summer and winter the slope was significantly lower than 1 (Table 3), which is lower than the slope expected if use was proportional to availability. This means that there is a trade-off situation in the use of agricultural land and pastures. When the availability of agricultural land and pastures was low, the animals selected for these habitat types, and used them less than expected when availability increased above a certain percentage. However, the slope was higher than 0, indicating that time spent in each habitat did increase with increasing availability, but not proportionally more. In summer the individuals used agricultural land and pasture less in relation to availability than in winter, as the red deer ceased to select for these habitat types at lower availabilities in summer. Removing animals that did not use agricultural land and pastures during the study period had no effect on the result (Table 3).

Table 3. Slopes (β), standard errors and slope + 1.96 SE of the proportions of use of agricultural land and pastures in relation to proportions of availability, grouped by season and type of tag/geographical area. All slopes were significantly lower than 1 with α = 0.05.

	All animals		Animals not using habitat type 1 & 2 removed	
	Sunnfjord	**Nordfjord**	**Sunnfjord**	**Nordfjord**
Summer				
β	0.583522	0.20355	0.51281	0.08796
SE	0.087364	0.10599	0.12745	0.13205
β + 1.96 SE	0.754755	0.41129	0.76261	0.34651
Winter				
β	0.39878	0.68780	0.39878	0.65834
SE	0.20528	0.14870	0.20528	0.14756
β + 1.96 SE	0.80112	0.97925	0.80113	0.94756

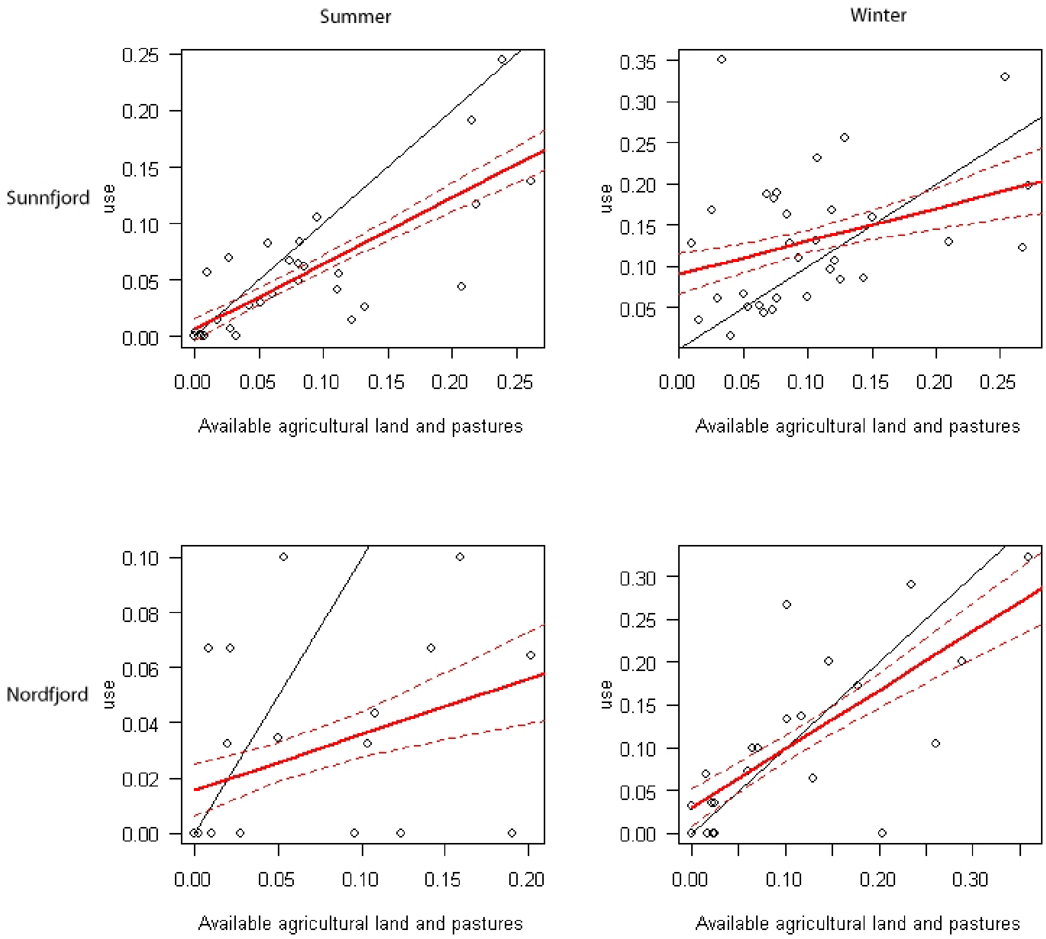

Figure 3. Plots showing trade-off situations in the use of agricultural land and pastures for 31 GPS-collared red deer in Sunnfjord and 22 VHF collared red deer in Nordfjord. Habitat type 1 and 2 are combined in this analysis. The x-axis shows proportions of available agricultural land and pastures, and the y-axis shows proportion of use of these habitat types. The points are individual red deer. The black line illustrates use proportional to availability (ß = 1), and the red line shows actual use in relation to availability by the red deer. The dotted lines represent 95% confidence limits.

3.3 Speed of movement

Speed per habitat type (Fig. 4) showed the same trends for all seasons. The deer generally moved fastest in forests of very high productivity, and slowest on pastures, confirming hypothesis H2c.

Based on an inspection of histograms looking for multiple peaks, there were no indications of distinct feeding or resting bouts in the various habitat types (see Appendix 4, Fig. A2).

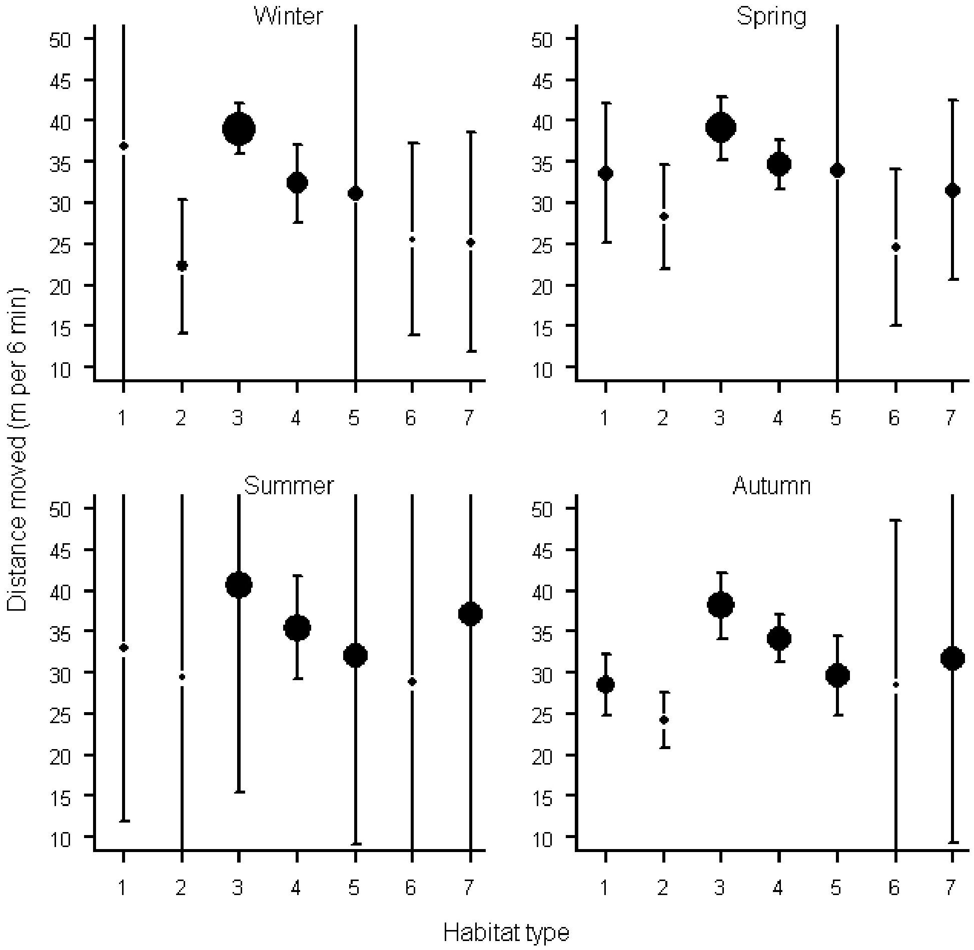

Figure 4. Mean speed (meters per 6 minutes) ± 95% confidence limits for 31 GPS-collared red deer in Sunnfjord, in relation to habitat type. The sizes of the points represent the number of observations in each habitat type. Numbers 1-7 specify the different habitat types, as shown in Fig. 2.

There were no significant differences in distance moved (m per 6 min) in relation to month (Fig. 5). There is a slight trend of increasing speed from February towards June, and then a slower speed from July towards October. January showed a somewhat higher speed than the rest of the year, but this is most likely a result of the small number of positions in January originating from a limited number of individuals.

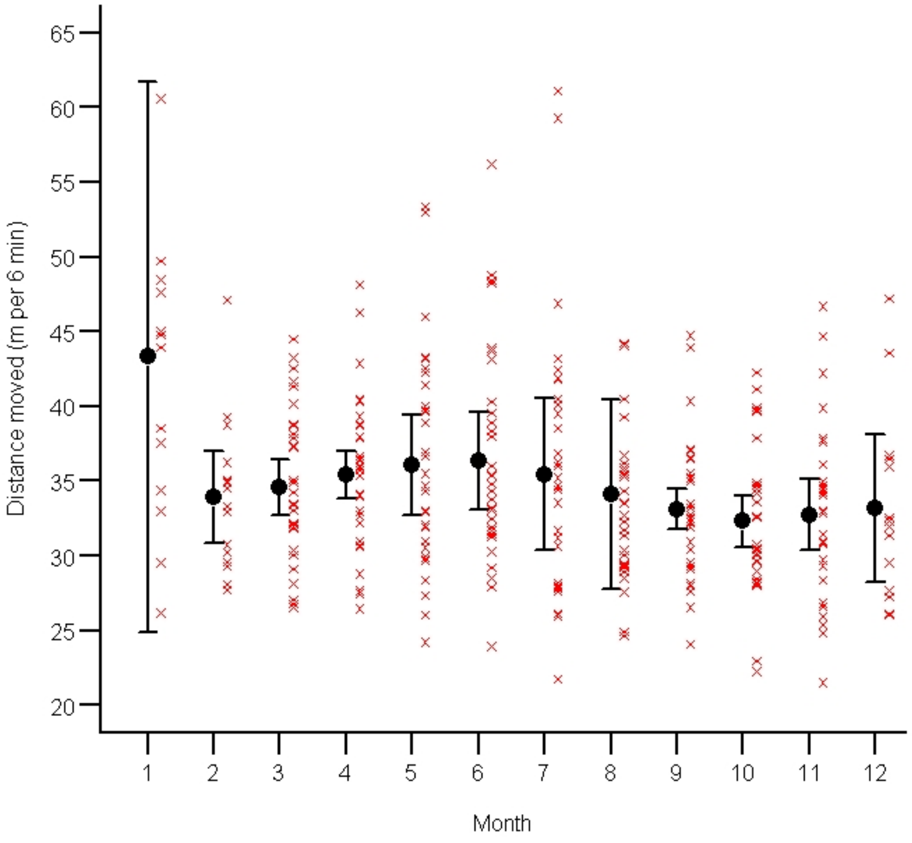

Figure 5. Mean speed (meters per 6 minutes) ± 95 % confidence limits for 31 GPS-collared red deer in Sunnfjord, in relation to months (1-12). Each red cross represents an individual red deer.

4 Discussion

Analyzing within home range scale habitat selection in red deer in Sogn og Fjordane, I found that, in consistency with hypothesis H1, the habitat selection changed through the seasons as would be expected if forage quality and quantity fluctuates through the year, and varies among habitats. Habitat selection also changed with time of day/state of activity, as predicted from hypothesis H2, suggesting a trade-off between forage availability and safety. Further evidence for a trade-off situation was found in the use of agricultural land and pastures, as the red deer selected for these habitat types when availability was low, and used them less than expected when they were more readily available.

4.1 Scales of temporal variation in habitat selection

Habitat selection is the outcome of selection for forage quality and quantity, as well as shelter (Ahlén, 1965; Langvatn & Hanley, 1993). The mechanisms determining habitat selection may vary with both temporal and spatial scale (Johnson, 1980; Morris, 1987; Senft *et al.*, 1987; Orians & Wittenberger, 1991). I have analyzed habitat selection at the within home range scale, and this may be dependent on shifts in daily and seasonal requirements of the animals. The requirements may be different depending for example on whether they are resting or foraging (daily scale) or on calving status (annual scale) (Mysterud, 1998), which can affect both energetic demands and selection for cover as a result of offspring being more vulnerable to predation. Overall RSFs are statistical descriptions, and provide little insight into why the animals select for certain habitats (Boyce & McDonald, 1999). I therefore distinguished between temporal scales in the analyses by comparing habitat selection in the various seasons (annual scale) and during different states of activity/times of day (daily scale) to identify the underlying mechanisms. On the daily scale, I found stronger selection of cover in daytime than in night-time, confirming hypothesis H2a. This pattern is commonly interpreted as a behavioural response to predator threats and climatic factors in ungulates (Mysterud & Østbye, 1999) and has earlier been reported in red deer (Catt & Staines, 1987), as well as in Rocky Mountain elk (*Cervus elaphus*) (Ager *et al.*, 2003), roe deer (*Capreolus capreolus*) (Mysterud, Lian & Hjermann, 1999b) and white-tailed deer (*Odocoileus virginianus*) (Beier & McCullough, 1990). On the annual scale, I found evidence for stronger selection of cover in summer, and for cultivated habitats in the remaining seasons, confirming hypothesis H1b. Similar selection for covered habitats in summer have also been found earlier in red deer (Carranza *et al.*, 1991) and in Rocky Mountain elk (Boyce *et al.*, 2003).

In this study, state of activity and time of day have been used together to infer patterns regarding short-term variation in selectivity. As the GPS-collars did not have activity-switches, I had to assume night-time was mainly in active state and daytime in inactive state. It has been shown several times that red deer (Georgii, 1981; Georgii & Schroder, 1983; Catt & Staines, 1987; Carranza *et al.*, 1991) and many other cervids (Cederlund, 1981; Beier & McCullough, 1990; Ager *et al.*, 2003) are mainly active during dusk and dawn, and in night-time (but se Clutton-Brock, Guinness & Albon (1982) for a different activity pattern). By comparing the locations obtained at the different times of day in the GPS-collars with the different states of activities recorded from the VHF-collars, it was possible to see if this statement was correct. The RSF-analysis showed similar patterns for both VHF- and GPS-collared individuals when daytime was compared to inactive state, and night-time to active state. This supports the assumption that the red deer are primarily active during dusk, dawn and night, and suggests that the approach of using state of activity and time of day together can be warranted.

4.1.1 Challenges and opportunities with GPS

GPS-technology holds advantages over more traditional methods of radio tracking, such as VHF, by allowing for consistent logging of large amounts of data through automated tracking. However, it should be noted that data obtained by remote sensing are prone to error. In GPS-collars, certain orientations of the collar are unfavorable, and can together with topography, vegetation and environmental conditions lead to variable fix-rates and location errors (D'Eon & Delparte, 2005; Graves & Waller, 2006). A fix-rate < 100%

leads to missing data, and may lead to biased selection estimates if locations are missed in some habitats more often than in others (D'Eon & Delparte, 2005). This is particularly a concern when comparing open habitats (such as agricultural land and pastures) with closed habitats (forests), like in my study. It is therefore important to be aware of this possible error when interpreting the results for analyses. The rate of successful fixes was high in this study (see Appendix 2, Table S1), suggesting that fix-rate bias is not a big concern. Also, the result of the RSF-analysis yielded similar patterns in habitat selection for both the VHF-collared red deer in Nordfjord and the GPS-collared red deer in Sunnfjord. In addition, selection for forests (closed habitats) was found in GPS-collared red deer. This is indicative for potential GPS-bias not being important in this study.

4.2 Habitat selection in a seasonal environment

As predicted by hypothesis H1, the red deer in this study selected habitats differently through the seasons, following the expected spatial and seasonal fluctuations in forage quality and quantity. Forage is generally of low availability and energetic quality through the winter, very abundant, nutritious and easy to digest in spring and early summer, before the quantity and quality declines again in autumn as plants senescence and lignify (Clutton-Brock, Guinness & Albon, 1982; Hofmann, 1989; Albon & Langvatn, 1992; Van Soest, 1994). The red deer and other ruminants prefer to feed on high quality forage. This yields more energy and protein per unit time, which also leads to less time spent ruminating, and in turn more time available for feeding (White, 1983). The changing quality and quantity of forage may affect the red deer's diet, and subsequently the variation in what is the most profitable habitat types. Snow levels may also influence habitat selection, as high snow cover can lead to higher energy expenditures in movement and seeking forage (Mysterud & Østbye, 1999).

Physiological changes in the red deer through the year are also likely to influence habitat selection. This have not been explicitly tested in this study, but according to earlier results, appetite, metabolic rate and productive activities like calving and neonatal care are adjusted to be in tune with the seasonal fluctuations in forage abundance

(Clutton-Brock *et al.*, 1982; Hofmann, 1989; Van Soest, 1994), and may influence patterns of habitat selection as well as movement rates.

4.2.1 Seasonal variation in covered and open habitats

Selection of agricultural land and pastures was higher in winter, spring and autumn than in summer, confirming hypothesis H1a. The seasonal variation in vegetation leads not only to variation in forage abundance, but also to shifting amounts of cover in the different habitats. Cover has indirect effects on forage (Mysterud & Østbye, 1999). By lowering the amount of light reaching the ground, forage quantity is reduced, and phenological growth is delayed. The cultivated fields are cut several times between June and late August, which increases the access to younger and more nutritious plant parts. As a result, agricultural habitats generally hold forage of high quality relative to forested habitats throughout the year, leading to the red deer more often selecting for these habitat types. Though not well quantified, the quality and quantity of forage in the forested areas likely approach that of agricultural land and pastures in summer due to higher productivity. This can explain the higher selection of covered areas in summer.

The difference in forage quality between the habitats is expected to be largest between winter and summer. This may explain why red deer are more prone to select for pastures during winter, as predicted by hypothesis H1b. Also, as forage occurring naturally is of limited availability and harder to find during winter, pastures provide the red deer with available forage that can be of relatively high energetic quality than most other types of forage that are quite readily available. This manner of habitat selection, which follows the seasonal variation in plant quality and quantity, increases the net intake of digestible energy.

Other habitat types, like marshland and bare mountains contain very little useful forage, as well as little to no cover for hiding, which can explain the avoidance and tendencies towards avoidance of these habitat types showed by the red deer.

4.2.2 Seasonality of speed

Habitat selection as inferred with RSFs does not provide explicit information on how much energy an animal gains in a specific habitat. Speed of movement through habitats can give an indication of the resource quality present (Morales *et al.*, 2004), and can therefore provide a valuable addition to the RSF analysis. However, it may also reflect how much time an animal spends resting vs. foraging. During all seasons, the red deer generally moved faster in forested than in cultivated habitats. Active behaviour is closely related to seeking and ingesting forage (Cederlund, 1981), and pastures hold a large quantity of highly nutritional forage for the red deer. This abundance should cause them to slow down the speed of movement, and increase time spent ingesting forage. In forested areas, good patches can be more unevenly distributed, and more time for seeking forage might be required compared to cultivated areas.

We observed no significant differences in speed of movement between fixes in relation to month. However, as predicted from hypothesis H1c, the means show a small trend in seasonal variation of speed through the year, which is in tune with the seasonal changes in quality and quantity of vegetation (Clutton-Brock *et al.*, 1982; Hofmann, 1989; Van Soest, 1994). The marginally decreased speed in autumn and winter compared to the other seasons, coincides with the drop in energetic quality and increased content of fibres in red deer diet, and with lower availability of forage (Van Soest, 1994). Also, physiological changes in the animals, like variations in appetite and metabolic rate through the year, can contribute to the trend shown in speed of movement. Seasonal variations in activity similar to the findings in this study have been found earlier in red deer (Georgii, 1981; Berger *et al.*, 2002), Rocky Mountain elk (Green & Bear, 1990), roe deer (Cederlund, 1981) and white-tailed deer (Beier & McCullough, 1990).

4.3 Trade-offs and daily patterns in habitat selection

The variation of forage characteristics through the year are not expected to induce daily patterns, as forage characteristics most likely vary little through the day. As predicted by hypothesis H2a, the red deer generally selected open habitats with abundant forage at night throughout the year, and safer habitats holding more cover but less forage, in daytime. My finding of a daily pattern in selection is likely caused by a trade-off commonly experienced by the red deer and many other organisms, which is between seeking cover in safe retreat habitats, and foraging in open habitats with abundant forage. Reasons for seeking covered habitats with less forage can be to escape potential predators, including humans, or to seek cover from climatic factors affecting the individual (Mysterud & Østbye, 1999). Covered habitats can relieve negative effects from heat and cold stress arising from temperature, wind and radiation, lower heat loss resulting from precipitation and decrease energy expenditure because of lower snow depth (Mysterud & Østbye, 1999). I argue that, as the shifts were quite consistent between day and night, and also with seasonal variations in forage and cover, this provides evidence for the trade-off being mainly between foraging and predation risk. The risk of predation can be lowered in covered habitats by functioning as protective cover reducing the chance of detection, and obstructive cover hindering vision and locomotion (Mysterud & Østbye, 1999). Natural predators predating on red deer are scarce in Norway, with golden eagles (*Aquila chrysaetos*) and lynx (*Lynx lynx*) being capable of killing calves (Bonenfant *et al.*, 2004). However, humans can be regarded as predators (Mysterud & Østbye, 1999), and pose a genuine threat, as hunting is the main cause of mortality of red deer in Norway.

4.3.1 Variations in the strength of trade-offs

The strength of the trade-off seemed to vary through the year, consistent with the seasonally varying abundance of forage and cover in the different habitats. In autumn, winter and spring, selection of open and covered habitats differed through the day, as adequate cover and highly nutritious forage are rarely found in the same habitat. In contrast, the shifting of habitats was less pronounced in summer, when vegetation is generally high and forage is abundant in forests as well. The increased use of covered habitat in summer can also be due to neonatal care of the red deer calves (Ager *et al.*, 2003), as these are usually born in or around June. Calves exhibit reduced mobility during this period, and staying in covered habitats could lower the risk of predation on the calves. This remains to be tested, as it is unknown whether or not females had calves in this study, but as females rarely miss to calf until they reach old age (Langvatn *et al.*, 2004), most females in our study likely had a calf at heel.

The red deer in this study demonstrated a functional response in selection of cultivated habitats, as predicted by hypothesis H2b. The functional response was apparent both in summer and winter, suggesting that they experience trade-offs involving habitat-specific, spatially segregated activities. The strength of the trade-off varied both with habitat availability and seasons. The time spent on agricultural land and pastures increased with increasing availability, but not proportionally more, leading to the strength of the trade-off varying with habitat availability. Related to seasons, the trade-off was more apparent in winter than in summer, as the red deer continued to select for agricultural land and pastures at higher availabilities in winter. This is probably a consequence of the distribution of forage and cover in the two seasons being different. The functional response is likely an antipredator behaviour that leads to as little exposure as possible in open habitats. Boyce *et al.* (2003) found that Rocky Mountain elk showed a similar use of upland grass and shrub land in winter, with selection of these vegetation types declining with increasing availability.

In this study, the open cultivated habitats are assumed to be the best areas for foraging through most of the year, and these habitats are also believed to be the most unsafe areas for the animals. The strong shifts in habitat selection shown here, altering between open and covered habitats holding different quality and quantity of forage, is expected to change the diets or energy budgets of the animals (Creel *et al.*, 2005). As shown in elk, highly nutritious forage on meadows was traded for lower quality forage in forests during the hunting season (Morgantini & Hudson, 1985). This means that the red deer and other animals in this situation trade off energy gain against the risk of predation when selecting habitats. Speed of movement through the various habitats support the apparent trade-off situation in habitat selection found in the RSF-analysis. With few exceptions, the red deer moved faster in the various forest types, and slowest on pastures. This is consistent with hypothesis H2c, predicting faster movement in more covered habitats. When travelling by a higher speed, relocating to forested habitats should lower the risk of detection by potential predators compared to open habitats.

5 Conclusion

This study of red deer habitat selection reminds us that habitat selection is a dynamic process. Seasonal variations in forage and cover, costs and benefits of the various habitat types and requirements of the animals are all important mechanisms affecting habitat selection. Resource selection functions are powerful tools to characterize habitat selection, and by extending the analyses by taking relevant temporal scales into account, the mechanisms behind habitat selection can be identified. At the daily scale, variation in habitat selection was most likely the outcome of different costs and benefits connected to forage and safety in the habitats, which provides support for the red deer experiencing trade-offs in habitat selection. On a seasonal scale, the high variation of forage quality and quantity between seasons, together with physiological changes in the animals, appears to have a large influence on red deer habitat selection, as they selected the habitats expected to hold the most nutritious forage. Cultivated habitats were frequently selected by the red deer in this study, and as these habitats are regarded to hold forage of relatively higher nutritional value than forage occurring naturally through most of the year, I argue that agricultural land and pastures are very important to the red deer.

I suggest that further studies should focus on the link between fitness and habitat selection by linking resource selection functions and the use of cultivated habitats to fitness related traits, such as body weight and calving rates. This will identify habitats critical for the survival and reproduction of the animals. This method have also been proven useful to identify trade-offs in lifetime reproductive success in red deer (McLoughlin *et al.*, 2006).

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Appendices

Appendix 1 – Size of error ellipses

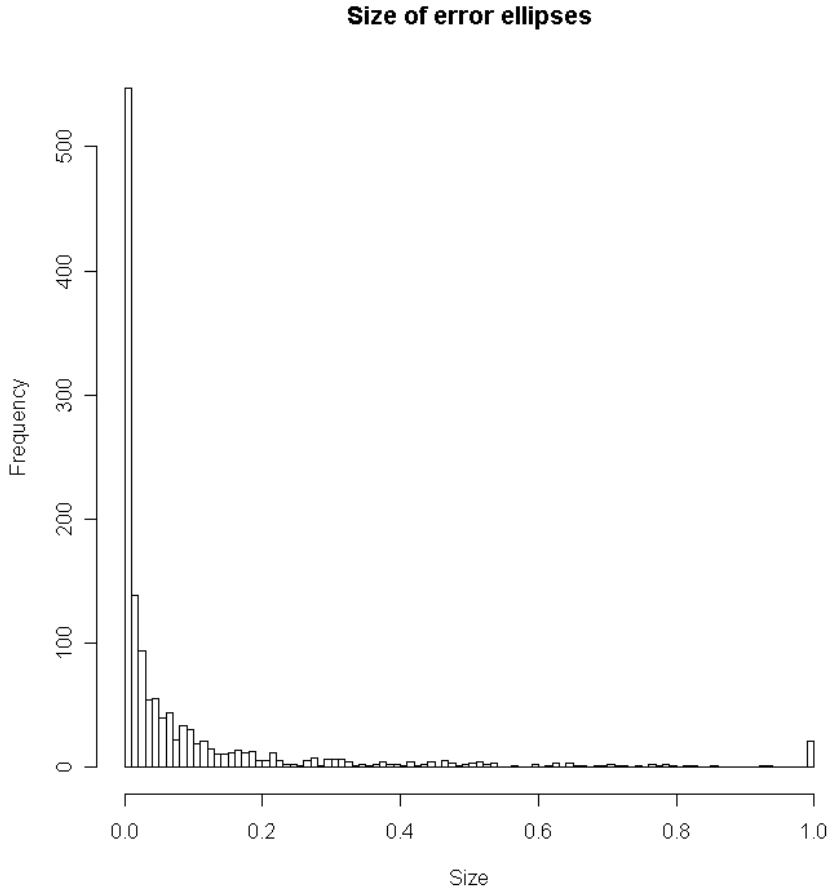


Figure A1. Distribution of the size of error ellipses for 22 VHF-collared red deer in Nordfjord, in km^2. All error ellipses larger than 1 km^2 (17) have been set to the size 1 km^2. As the size was generally low, all locations were included in the analyses.

Appendix 2 – GPS success rate

Table A1. Individual and overall success rates (successful divided by attempted fixes) of GPS-collars.

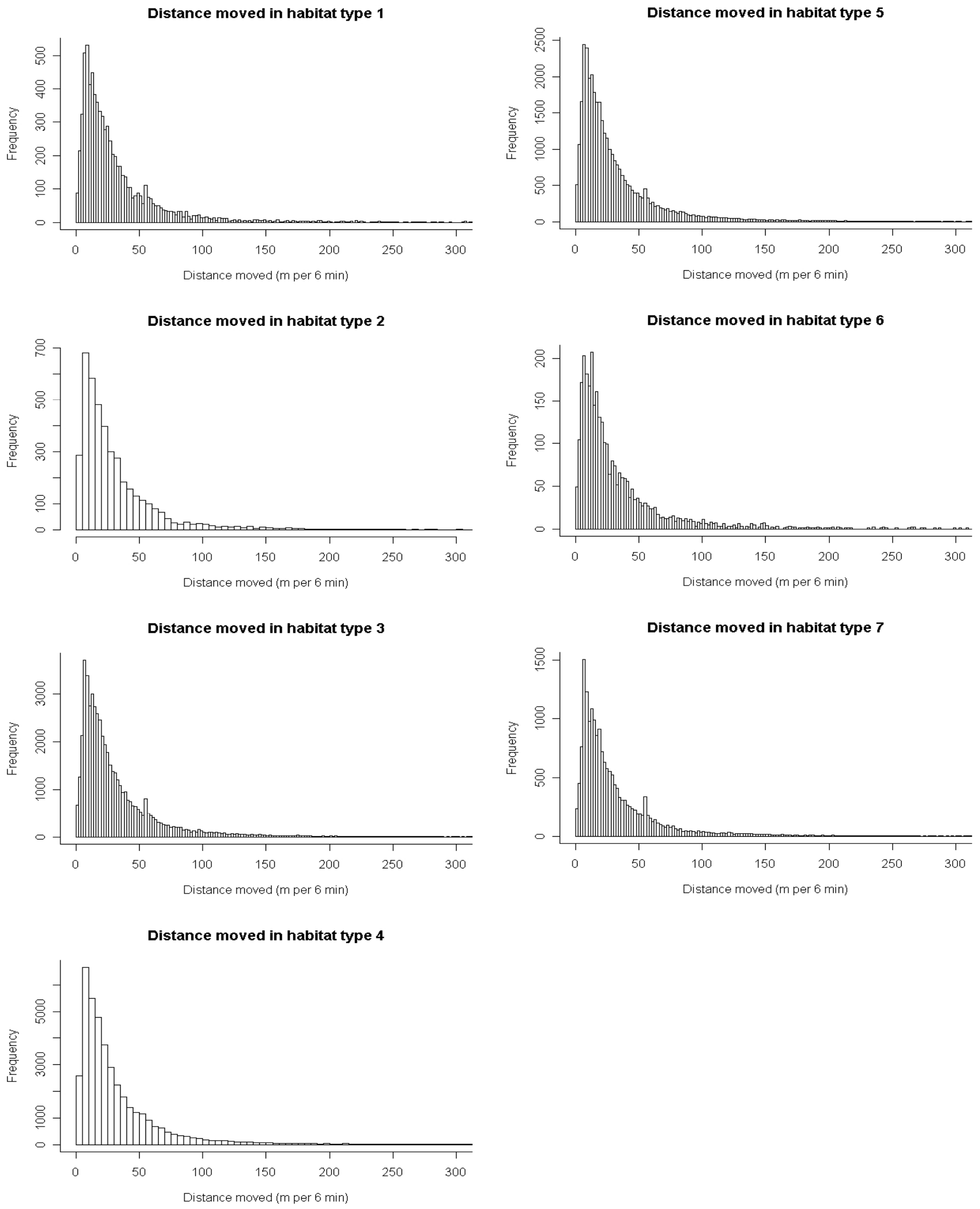
Frequency	Year	Attempted	Success	Success rate
142009	2005	16583	15170	91
142021	2005		Early mortality	
142034	2005	16583	15371	93
142034	2006	11868	11689	98
142045	2005	16636	14796	89
142074	2005	14676	12975	88
142088	2005	12053	9249	77
142119	2005	14590	11598	79
142175	2005	10700	9310	87
142175	2006	11868	10127	85
142205	2005	16462	14707	89
142205	2006	12419	10598	85
142215	2005	15672	12720	81
142224	2005	16571	14353	87
142250	2005	15769	14480	92
142250	2006	12780	11872	93
142259	2005	15219	14080	93
142269	2005	15765	14149	90
142280	2005	15426	14799	96
142339	2005	14042	12637	90
142350	2005	13249	12810	97
142350	2006	12971	11949	92
142360	2005	14040	13466	96
142385	2005	14699	13908	95
142395	2005	15057	13606	90
142395	2006	12399	11456	92
142422	2005	13994	13354	95
142434	2005	13995	12062	86
142434	2006	12971	12185	94
142445	2005	13987	12886	92
142455	2006	13824	12397	90
	Mean:	**14229**	**12825**	**90**

Appendix 3 – Classification of the seasons

Table A2. Monthly classification of the seasons.

Season	**Start**	**End**
Winter	December 1st	March 31st
Spring	April 1st	May 31st
Summer	June 1st	August 15th
Autumn	August 16th	November 30th

Appendix 4 – Distributions of speed in relation to habitat type


Distance moved in habitat type 1

Distance moved in habitat type 5

Distance moved in habitat type 2

Distance moved in habitat type 6

Distance moved in habitat type 3

Distance moved in habitat type 7

Distance moved in habitat type 4

Figure A2. Frequency of distance categories (meters per 6 minutes) in each habitat type. Data are pooled for 31 GPS-collared red deer in Sunnfjord. Numbers 1-7 specify the different habitat types, as shown in Fig. 2.