

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

INGER MAREN RIVRUD GODVIK,¹ LEIF EGIL LOE,¹ JON OLAV VIK,^{1,3} VEBJØRN VEIBERG,^{1,2} ROLF LANGVATN,²
AND ATLE MYSTERUD^{1,4}

¹Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biology, University of Oslo, P.O. Box 1066 Blindern, N-0316 Oslo, Norway

²Norwegian Institute for Nature Research, Tungasletta 2, N-7085 Trondheim, Norway

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 (Orlans 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

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

³Present address: Centre for Integrative Genetics (CI-GENE), Norwegian University of Life Sciences, P.O. Box 5003, N-1432 Ås, Norway.

⁴Corresponding author. E-mail: atle.mysterud@bio.uio.no

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 (Myserud 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 (Myserud 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 (Myserud 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 (Myserud et al. 2000).

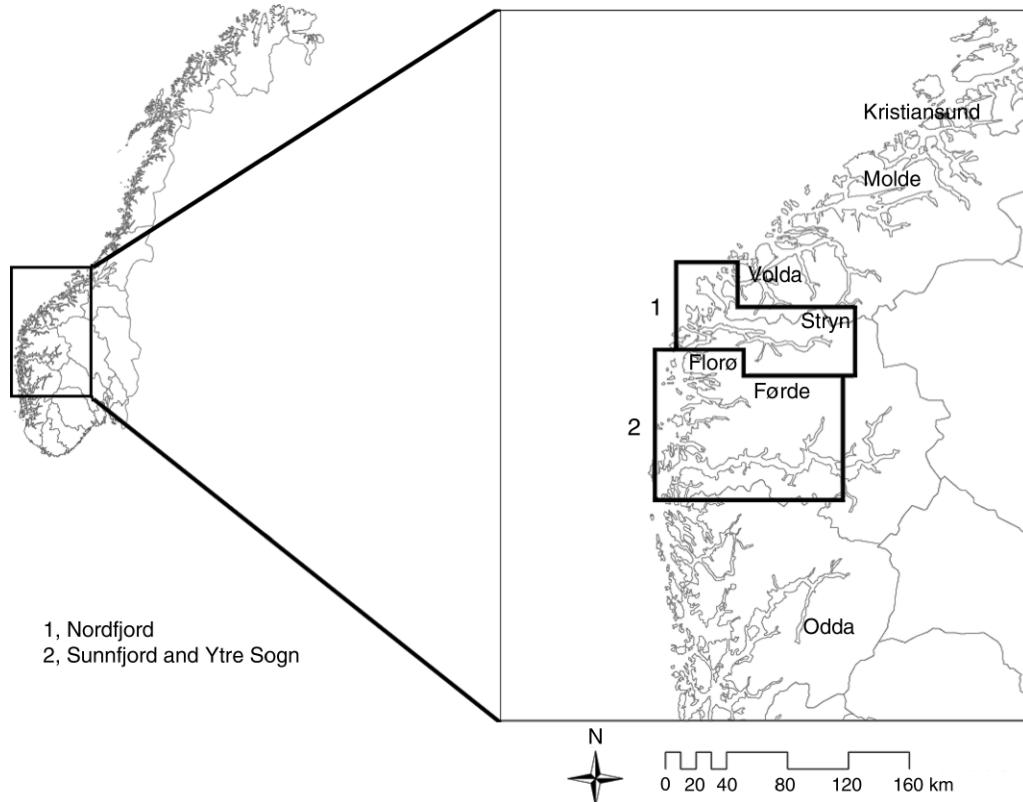


FIG. 1. Map of the study area situated in the western part of southern Norway. Boxes represent the different regions inhabited by the red deer (*Cervus elaphus*) in this study.

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, Lindsberg, 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, Lindsberg, 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

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

where observations $i = 1 \dots n$ are clustered within strata $j = 1 \dots m$; 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 λ_{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;

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.

Variable	β	SE	HPD interval bounds	
			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: $N_{\text{obs}} = 138\,876$ observed locations from GPS collars; $N_{\text{av}} = 133\,865$ 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

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; $SD = 2.2 \times 10^{-5}$ [HPD interval 4.3×10^{-12} – 1.0×10^{-7}]). HPD intervals are the highest posterior density intervals (Plummer et al. 2007). $N_{\text{obs}} = 1284$ observed locations from GPS collars; $N_{\text{av}} = 42571$ 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 \mathbf{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 \mathbf{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

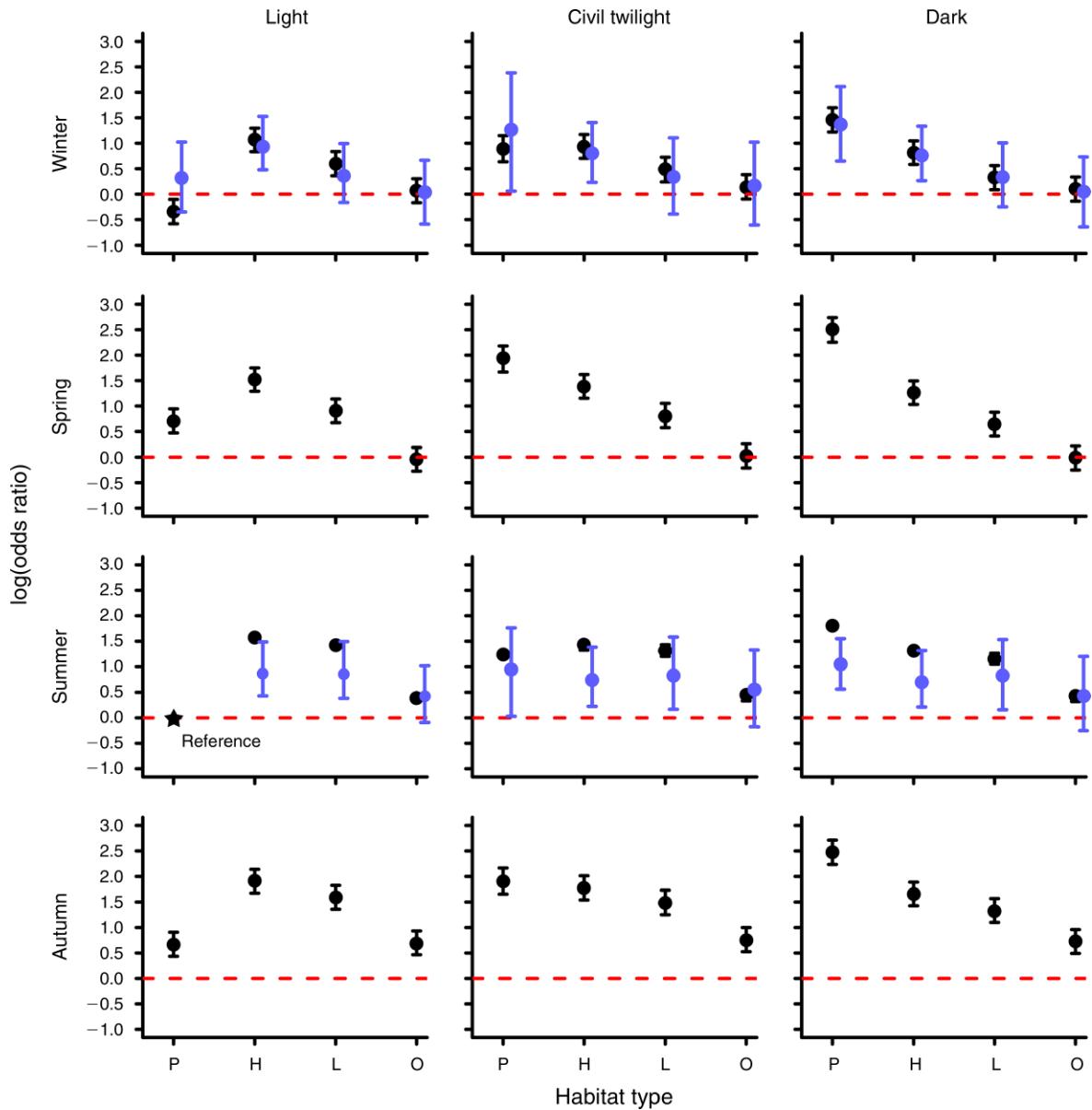


FIG. 2. Comparing habitat selection through different seasons and light intensities for 62 female red deer in Norway. Estimates are log odds ratios \pm 95% highest posterior density intervals, where the log odds ratios are calculated relative to selection of pastures in summer during daylight (reference 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,

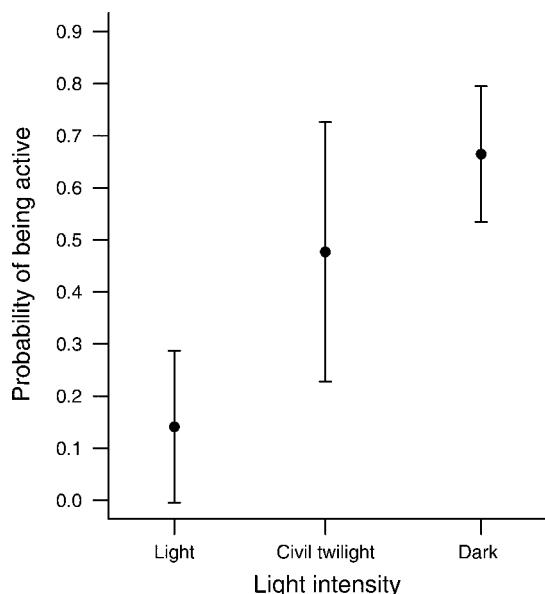


FIG. 3. Probability of being active (mean \pm SE) as a function of light condition (light, civil twilight, and dark), for 22 VHF-collared female red deer in Norway. Activity was recorded based on the pulse rate of VHF collars (see *Materials and methods*).

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 .

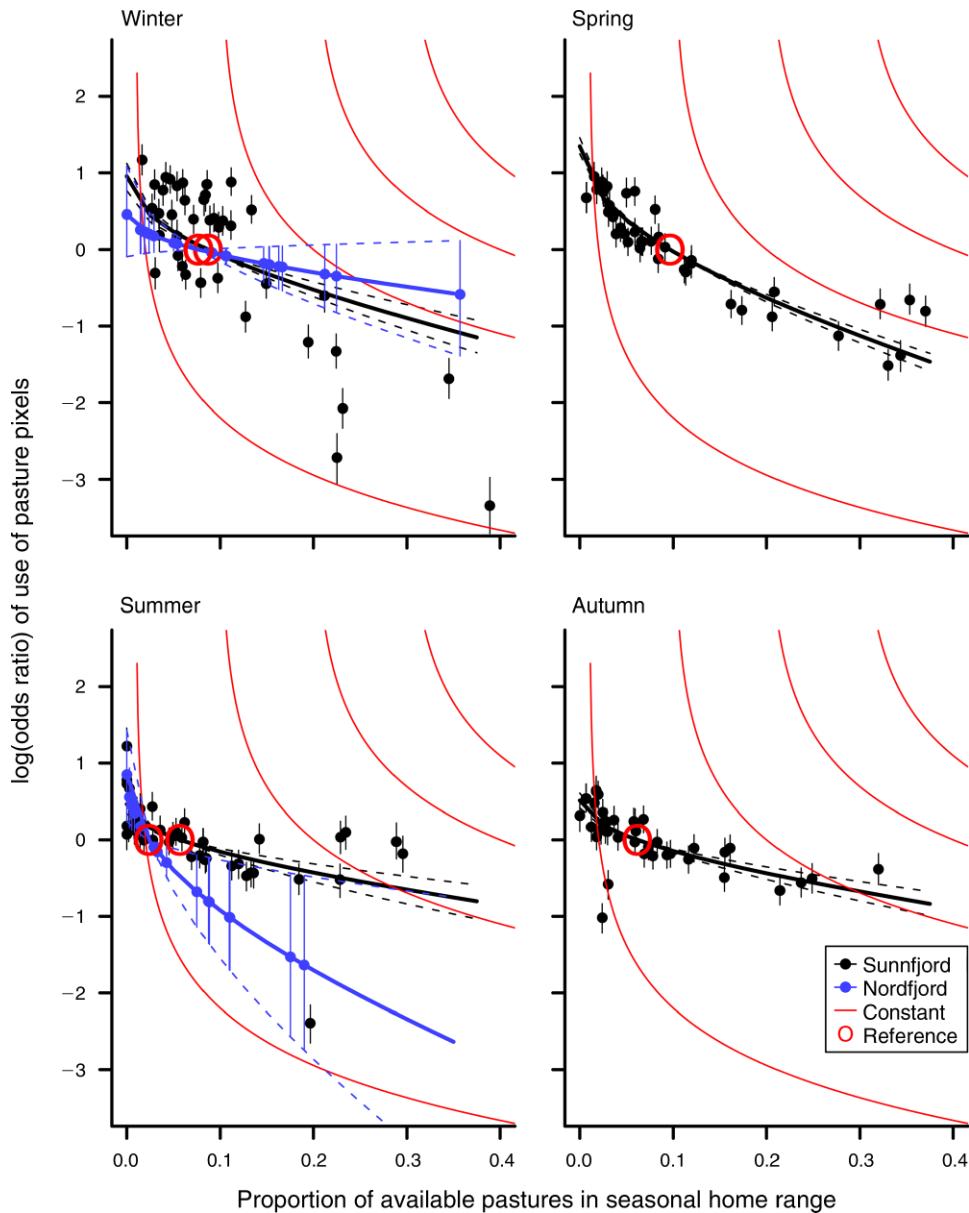


FIG. 4. Functional responses in the selection of pastures for 62 red deer in Norway (Sunnfjord/GPS, black symbols and lines; Nordfjord/VHF, blue symbols and lines). The log odds ratios of the use of pasture pixels are calculated relative to average available pastures in the seasonal home range (red circles) 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 Licope on a previous draft.

LITERATURE CITED

- Abrahamsen, J., N. K. Jacobsen, R. Kalliola, E. Dahl, L. Wilborg, and L. Pålsson. 1977. Naturgeografisk regioninndeling av Norden. Nordiske Utredninger Series B 34:1–135.
- Ager, A. A., B. K. Johnson, J. W. Kern, and J. G. Kie. 2003. Daily and seasonal movements and habitat use by female Rocky Mountain elk and mule deer. *Journal of Mammalogy* 84:1076–1088.
- Albon, S. D., and R. Langvatn. 1992. Plant phenology and the benefits of migration in a temperate ungulate. *Oikos* 65:502–513.
- Armleder, H. M., M. J. Waterhouse, D. G. Keisker, and R. J. Dawson. 1994. Winter habitat use by mule deer in the central interior of British Columbia. *Canadian Journal of Zoology* 72:1721–1725.
- Armstrong, E., D. Euler, and G. Racey. 1983. White-tailed deer habitat and cottage development in central Ontario. *Journal of Wildlife Management* 47:605–612.
- Bates, D. M. 2006. lmer, *P*-values and all that. (<https://stat.ethz.ch/pipermail/r-help/2006-May/094765.html>)

- Bates, D. M. 2007. lme4: Linear mixed-effects models using Eigen and Eigen. R package version 0.99875-9.
- Beier, P., and D. R. McCullough. 1988. Motion-sensitive radio collars for estimating white-tailed deer activity. *Journal of Wildlife Management* 52:11–13.
- Beier, P., and D. R. McCullough. 1990. Factors influencing white-tailed deer activity patterns and habitat use. *Wildlife Monographs* 109:5–51.
- Boyce, M. S., J. S. Mao, E. H. Merrill, D. Fortin, M. G. Turner, J. Fryxell, and P. Turchin. 2003. Scale and heterogeneity in habitat selection by elk in Yellowstone National Park. *Ecoscience* 10:421–431.
- Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. *Ecological Modelling* 157:281–300.
- Carranza, J., S. J. H. Detruicios, R. Medina, J. Valencia, and J. Delgado. 1991. Space use by red deer in a Mediterranean ecosystem as determined by radio-tracking. *Applied Animal Behaviour Science* 30:363–371.
- Catt, D. C., and B. W. Staines. 1987. Home range use and habitat selection by red deer (*Cervus elaphus*) in a Sitka spruce plantation as determined by radio-tracking. *Journal of Zoology* 211:681–693.
- Cederlund, G. 1981. Daily and seasonal activity pattern of roe deer in a boreal habitat. *Viltrevy* 11:315–353.
- Clutton-Brock, T. H., F. E. Guinness, and S. D. Albon. 1982. Red deer: behavior and ecology of the two sexes. University of Chicago Press, Chicago, Illinois, USA.
- D'Eon, R. G. 2003. Effects of a stationary GPS fix-rate bias on habitat selection analyses. *Journal of Wildlife Management* 67:858–863.
- D'Eon, R. G., and D. Delparte. 2005. Effects of radio-collar position and orientation on GPS radio-collar performance, and the implications of PDOP in data screening. *Journal of Applied Ecology* 42:383–388.
- D'Eon, R. G., R. Serrouya, G. Smith, and C. O. Kochanny. 2002. GPS radiotelemetry error and bias in mountainous terrain. *Wildlife Society Bulletin* 30:430–439.
- ESRI. 2006. ArcMAP 9.2. ESRI (Environmental Systems Research Institute). Redlands, California, USA.
- Frair, J. L., S. E. Nielsen, E. H. Merrill, S. R. Lele, M. S. Boyce, R. H. M. Munro, G. B. Stenhouse, and H. L. Beyer. 2004. Removing GPS collar bias in habitat selection studies. *Journal of Applied Ecology* 41:201–212.
- Georgii, B. 1981. Activity patterns of female red deer (*Cervus elaphus* L.) in the Alps. *Oecologia* 49:127–136.
- Georgii, B., and W. Schroder. 1983. Home range and activity patterns of male red deer (*Cervus elaphus* L.) in the Alps. *Oecologia* 58:238–248.
- Gillies, C. S., M. Hebblewhite, S. E. Nielsen, M. A. Krawchuk, C. L. Aldridge, J. L. Frair, D. J. Saher, C. E. Stevens, and C. L. Jerde. 2006. Application of random effects to the study of resource selection by animals. *Journal of Animal Ecology* 75:887–898.
- Gillingham, M. P., K. L. Parker, and T. A. Hanley. 1997. Forage intake by black-tailed deer in a natural environment: bout dynamics. *Canadian Journal of Zoology* 75:1118–1128.
- Gordon, I. J., A. J. Hester, and M. Festa-Bianchet. 2004. The management of wild large herbivores to meet economic, conservation and environmental objectives. *Journal of Applied Ecology* 41:1021–1031.
- Graves, T. A., and J. S. Waller. 2006. Understanding the causes of missed global positioning system telemetry fixes. *Journal of Wildlife Management* 70:844–851.
- Hansen, M. C., G. W. Garner, and S. G. Fancy. 1992. Comparison of 3 methods for evaluating activity of Dall sheep. *Journal of Wildlife Management* 56:661–668.
- Hebblewhite, M., and E. Merrill. 2008. Modeling wildlife-human relationships for social species with mixed-effects resource selection models. *Journal of Applied Ecology* 45: 834–844.
- Jenkins, D. A., J. A. Schaefer, R. Rosatte, T. Bellhouse, J. Hamr, and F. F. Mallory. 2007. Winter resource selection of reintroduced elk and sympatric white-tailed deer at multiple spatial scales. *Journal of Mammalogy* 88:614–624.
- Johnson, B. K., J. W. Kern, M. J. Wisdom, S. L. Findholt, and J. G. Kie. 2000. Resource selection and spatial separation of mule deer and elk during spring. *Journal of Wildlife Management* 64:685–697.
- Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65–71.
- Langvatn, R., S. D. Albon, T. Burkey, and T. H. Clutton-Brock. 1996. Climate, plant phenology and variation in age of first reproduction in a temperate herbivore. *Journal of Animal Ecology* 65:653–670.
- Lemaitre, J., and M. A. Villard. 2005. Foraging patterns of pileated woodpeckers in a managed Acadian forest: a resource selection function. *Canadian Journal of Forest Research* 35:2387–2393.
- Lima, S. L., and P. A. Bednekoff. 1999. Temporal variation in danger drives antipredator behavior: The predation risk allocation hypothesis. *American Naturalist* 153:649–659.
- Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68:619–640.
- Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Second edition. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Mauritzen, M., S. E. Belikov, A. N. Boltunov, A. E. Derocher, E. Hansen, R. A. Ims, O. Wiig, and N. Yoccoz. 2003. Functional responses in polar bear habitat selection. *Oikos* 100:112–124.
- McLoughlin, P. D., M. S. Boyce, T. Coulson, and T. Clutton-Brock. 2006. Lifetime reproductive success and density-dependent, multi-variable resource selection. *Proceedings of the Royal Society B* 273:1449–1454.
- McShea, M. J., H. B. Underwood, and J. H. Rappole. 1997. The science of overabundance: deer ecology and population management. Smithsonian Institution Press, Washington, D.C., USA.
- Morgantini, L. E., and R. J. Hudson. 1985. Changes in diets of wapiti during a hunting season. *Journal of Range Management* 38:77–79.
- Morris, D. W. 1987. Ecological scale and habitat use. *Ecology* 68:362–369.
- Mysterud, A., and R. A. Ims. 1998. Functional responses in habitat use: availability influences relative use in trade-off situations. *Ecology* 79:1435–1441.
- Mysterud, A., P. K. Larsen, R. A. Ims, and E. Ostbye. 1999. Habitat selection by roe deer and sheep: does habitat ranking reflect resource availability? *Canadian Journal of Zoology* 77: 776–783.
- Mysterud, A., and E. Østbye. 1999. Cover as a habitat element for temperate ungulates: effects on habitat selection and demography. *Wildlife Society Bulletin* 27:385–394.
- Mysterud, A., N. G. Yoccoz, N. C. Stenseth, and R. Langvatn. 2000. Relationships between sex ratio, climate and density in red deer: the importance of spatial scale. *Journal of Animal Ecology* 69:959–974.
- Nielsen, S. E., M. S. Boyce, G. B. Stenhouse, and R. H. M. Munro. 2002. Modeling grizzly bear habitats in the Yellowstone ecosystem of Alberta: taking autocorrelation seriously. *Ursus* 13:45–56.
- Orians, G. H., and J. F. Wittenberger. 1991. Spatial and temporal scales in habitat selection. *American Naturalist* 137: S29–S49.
- Osko, T. J., M. N. Hiltz, R. J. Hudson, and S. M. Wasel. 2004. Moose habitat preferences in response to changing availability. *Journal of Wildlife Management* 68:576–584.

- Parker, K. L., C. T. Robbins, and T. A. Hanley. 1984. Energy expenditures for locomotion by mule deer and elk. *Journal of Wildlife Management* 48:474–488.
- Plummer, M., N. Best, K. Cowles, and K. Vines. 2007. CODA: output analysis and diagnostics for MCMC. R package version 0.12-1. (<http://www.r-project.org/>)
- Poole, K. G., and G. Mowat. 2005. Winter habitat relationships of deer and elk in the temperate interior mountains of British Columbia. *Wildlife Society Bulletin* 33:1288–1302.
- R Development Core Team. 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Reckardt, K., and G. Kerth. 2007. Roost selection and roost switching of female Bechstein's bats (*Myotis bechsteini*) as a strategy of parasite avoidance. *Oecologia* 154:581–588.
- Rosenzweig, M. L. 1981. A theory of habitat selection. *Ecology* 62:327–335.
- Senft, R. L., M. B. Coughenour, D. W. Bailey, L. R. Rittenhouse, O. E. Sala, and D. M. Swift. 1987. Large herbivore foraging and ecological hierarchies. *BioScience* 37:789–799.
- Sih, A. 1980. Optimal foraging: Can foragers balance two conflicting demands? *Science* 210:1041–1043.
- Skrondal, A., and S. Rabe-Hesketh. 2004. Generalized latent variable modeling: multilevel, longitudinal, and structural equation models. Chapman and Hall, New York, New York, USA.
- Van Soest, P. J. 1994. Nutritional ecology of the ruminant. Second edition. Cornell University Press, New York, New York, USA.
- Werner, E. E., J. F. Gilliam, D. J. Hall, and G. G. Mittelbach. 1983. An experimental test of the effects of predation risk on habitat use in fish. *Ecology* 64:1540–1548.
- White, G. C., and R. A. Garrott. 1990. Analysis of wildlife radio-tracking data. Academic Press, London, UK.
- Wood, S. N. 2006. Generalized additive models: an introduction with R. Chapman and Hall/CRC, Boca Raton, Florida, USA.

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).