

The impacts of landscape structure on the winter movements and habitat selection of female red deer

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Abstract An area of research that has recently gained more attention is to understand how species respond to environmental change such as the landscape structure and fragmentation. Movement is crucial to select habitats but the landscape structure influences the movement patterns of animals. Characterising the movement characteristics, utilisation distribution (UD) and habitat selection of a single species in different landscapes can provide important insights into species response to changes in the landscape. We investigate these three fields in female red deer (*Cervus elaphus*) in southern Sweden, in order to understand how landscape structure influences their movement and feeding patterns. Movements are compared between two regions, one dominated by a fragmented agriculture–forest mosaic and the other by managed homogenous forest. Red deer in the agriculture-dominated landscape had larger UDs compared to those in the forest-dominated area, moved larger distances between

feeding and resting and left cover later in the day but used a similar duration for their movements, suggesting faster travelling speeds between resting and feeding locations. The habitat selection patterns of red deer indicate a trade-off between forage and cover, selecting for habitats that provide shelter during the day and forage by night. However, the level of trade-off, mediated through movement and space use patterns, is influenced by the landscape structure. Our approach provides further understanding of the link between individual animal space use and changing landscapes and can be applied to many species able to carry tracking devices.

Keywords Animal movement · Biased-random bridge · Landscape ecology · Net-squared displacement · Resource utilisation function · Wildlife management

Introduction

One area of research that has recently gained more attention is to understand how animals respond to the composition and spatial configuration of the landscape (i.e. landscape structure; McGarigal and McComb 1995) and how environmental change influences their movement patterns (Johnson et al. 1992; Morales et al. 2010). Animals move, amongst other things, to acquire resources, to reproduce and to avoid predators or competition with conspecifics (Turchin 1998; Fahrig 2007). Therefore, changes in the landscape structure such as the availability of resources, patch size and connectivity will influence animal movements, due to factors such as the ability to find food or shelter and the need to move between them on a seasonal and daily basis (O'Neill et al. 1988; Mysterud and Ims 1998; Rivrud et al. 2010).

Movement ecology provides a number of insights into potential responses to landscape change. Home range studies have shown that roe deer (*Capreolus capreolus*) are required

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to range over larger areas when resource availability is low (Tufto et al. 1996). Such patterns are also supported by theoretical work that animals moving through a habitat with low resource availability will have straighter and quicker movements, as the animal searches for higher-quality habitats (Fahrig 2007). Research into red deer (*Cervus elaphus*) habitat selection indicates that the relative use of a habitat changes according to its availability, a process known as functional responses in habitat selection (Myserud and Ims 1998; Godvik et al. 2009). Therefore, as seasons or humans modify the proportion of habitats in the landscape and resource availability, one can expect the selection of preferred habitats to increase as their availability decreases. The pattern of selection may also vary with the daily rhythm of feeding and resting, as Godvik et al. (2009) show that open habitats are favoured at night when red deer are feeding whilst closed habitats are favoured during the day when red deer are resting, an activity pattern that may be a response to human disturbance (Georgii 1981; Clutton-Brock et al. 1982; Pépin et al. 2009). These studies indicate how research into habitat selection and movement characteristics of a species can be important tools for understanding species adaptations to changes in the landscape.

Recent studies have focused on either large-scale yearly patterns of moose and red deer movement in relation to phenology (Bischof et al. 2012; van Moorter et al. 2013) or on small-scale red deer habitat selection that depended on home range estimates and the time of day used as a proxy for feeding and resting phases (Rivrud et al. 2010). Here we present a study on animal movement that aims to understand how differences in the landscape structure in two study areas (agriculture- versus forest-dominated) influence the daily movement of a species (the timing, duration and distance). The study uses a unified framework that links movement and habitat selection patterns of a species, thus contributing to advancing the conceptual framework of movement ecology (Nathan et al. 2008). Our methodology distinguishes between movement and stationary phases using an objective and model-driven approach (Bunnefeld et al. 2011; Börger and Fryxell 2012), and thus divides an animal's movement between feeding and resting periods, providing results that link to first principals of an animal's internal state and its interaction with biotic and abiotic factors (Nathan et al. 2008).

The red deer system in Sweden is an ideal case study, as the species is managed in contrasting landscapes of forest-dominated areas to a fragmented mosaic of agriculture with smaller forest patches. The knowledge gained from this study will not only improve our understanding of animal movement in response to landscape and environmental changes but will also contribute to formulating future management plans. This is of particular interest for a species such as the red deer, whose population has increased dramatically in recent decades and involves different stakeholders with competing

objectives; it is a valuable game species (high-density desirable) but can cause considerable costs to forestry through browsing damage (low-density desirable; Milner et al. 2006; Apollonio et al. 2010; Månsson and Jarnemo 2013). Combining movement ecology and habitat selection provides a unique opportunity to improve our understanding and assess its effectiveness within a comparable framework of wild red deer occurring in structurally different landscapes.

Study site

This study was undertaken in two regions of southern Sweden (Fig. 1). Skåne (N55°65E13°50) is the southernmost county (hereafter South) and Södermanland–Östergötland (N58°75E16°40) is in the southeast (hereafter North). The dominant habitat type in the South is agricultural land covering 45 % of the landscape whilst forests only cover 35 %. Norway spruce is the main forest type (38 %) followed by broadleaf forests (35 %; Skogsdata 2011). In contrast, the North's landscape is mainly covered by forests (55 %) and agricultural land is only 20 %. Forests in the North are predominately split between Scots pine (32 %), Norway spruce (28 %) and mixed conifer forests (18 %; Skogsdata 2011). The mean annual temperature in the South is 6.5 °C with mean annual precipitation of 800 mm (WMO normal period 1961–1990; SMHI 2012). During the same period, the average number of snow days per year was 40 with a mean max depth of 10 cm (SMHI 2012). In the North, the mean annual temperature is 5.5 °C with mean annual precipitation of 787 mm (WMO normal period 1961–1990; SMHI 2012). During the same period, the average number of snow days per year was 80 with a mean max depth of 35 cm (SMHI 2012). The density of red deer in the two study sites are unknown; however, harvest data indicates that the density of red deer is higher in the North study site due to a greater number of individuals harvested per 1,000 ha (Månsson and Jarnemo 2013).

Methods

We used the approach outlined by Papworth et al. (2012) linking net-squared displacement to identify movement, resting and feeding phases, utilisation distribution (UD) to quantify the area used during the three phases and the resource utilisation function (RUF) to analyse habitat selection (Fig. 2).

Movement data

Red deer hinds were fitted with a Global Positioning System (GPS) collar (Vectronic Aerospace PRO Light 3D) and a

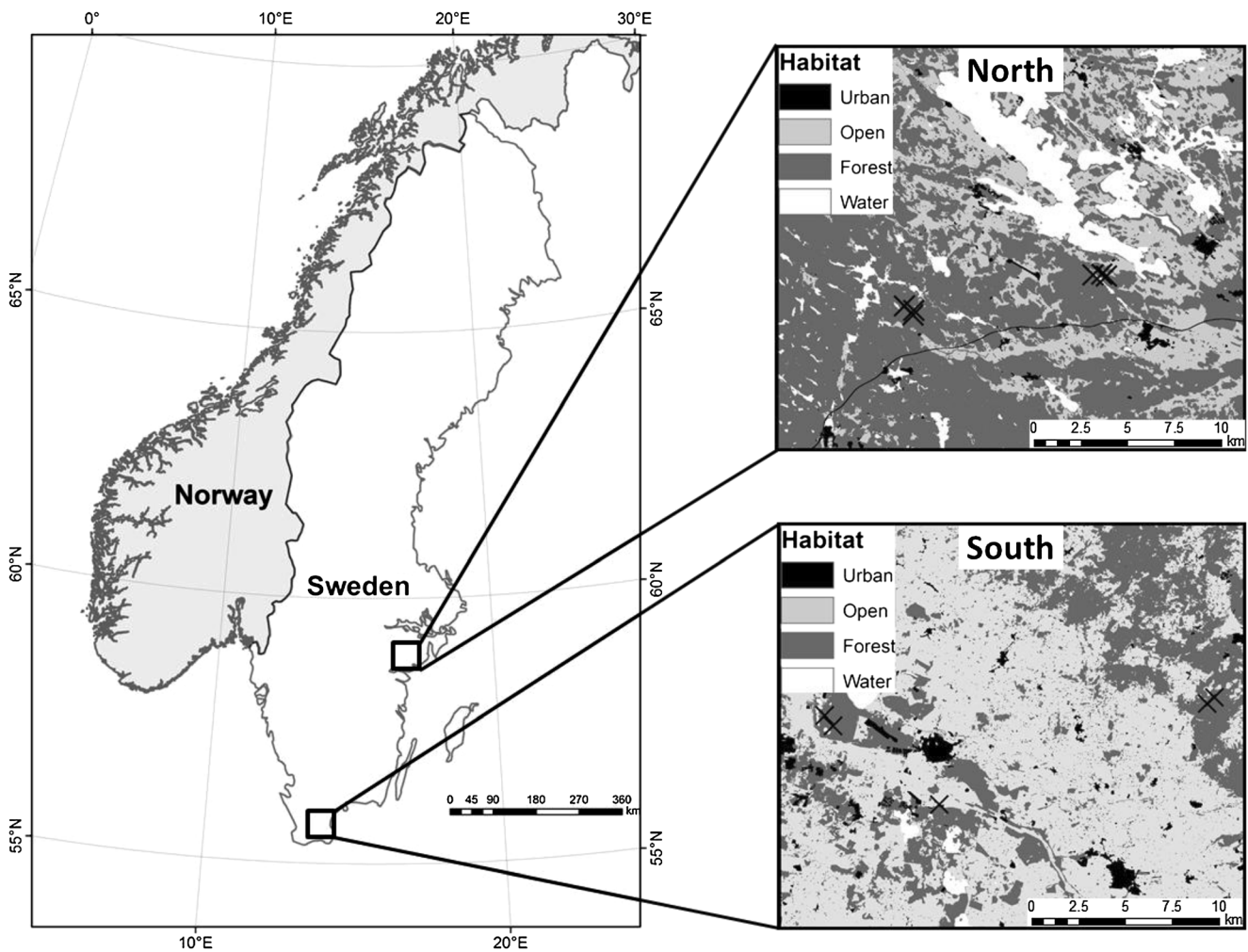


Fig. 1 Map showing the locations of the two study sites in Sweden (*left*) and the habitat composition in the North study site (*top right*) and South study site (*bottom right*). The symbol “X” indicates the average location of an individual red deer during the study period

plastic ear tag for identification. Only adult hinds (at least 2 years old) were fitted with a collar; however, the exact age of collared deer is unknown. Handling protocols were examined by the animal ethics committee for central Sweden and fulfilled the ethical requirements for research on wild animals (decisions M258-06 and 50–06). Data is available for 12 red deer, containing six individuals from each study area. GPS locations were recorded during the winter months of January, February and March 2008, and locations were recorded every 15 min once a week. The GPS data was screened using the method outlined by Bjørneraas et al. (2010; Online Resource 1). Hunting in both regions caused deer to travel several kilometres before returning back to the study site a few days later (Jarnemo and Wikenros 2014). Hunting dates were provided for both regions; therefore, the data was further screened to remove movements on these dates. The remaining sample size for statistical analysis contained 6,521 locations in the South and 5,308 locations in the North.

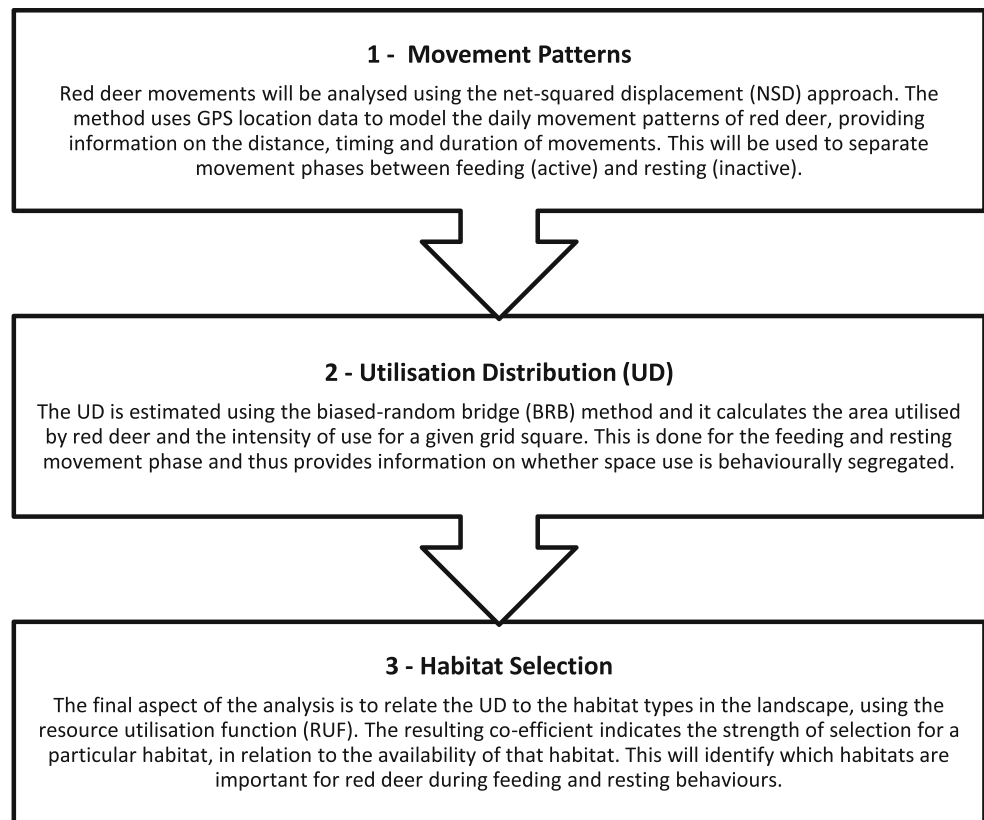
Habitat data

Habitat maps were generated using ArcMap version 9.3.1 (ESRI 2009) with shapefiles that contained ground cover information generated by Svenska Marktäckedata (Hagner et al. 2005). The ground cover maps were last updated in 2002 and have a resolution of 25 m×25 m. The map was updated with data of harvested forest stands (clear fellings) available for the years 2003 to 2005 (from the Swedish forestry board). The ground cover maps were used in the home range and habitat selection analysis.

Movement modelling

We modify the approach used by Papworth et al. (2012) as red deer are not known as central place foragers, i.e. they do not leave from or return to the same feeding or resting area on a regular basis. However, previous research has shown that their habitat use does vary in space and time, showing preference

Fig. 2 Methodology framework for the analysis of red deer movement patterns and feeding decisions



for closed sheltered habitats during resting bouts and open habitats during active foraging bouts (Georgii 1981; Green and Bear 1990; Mysterud and Ims 1998; Godvik et al. 2009). Studies have also shown that deer are normally active at dusk or dawn and at night and inactive during the day (Georgii 1981; Green and Bear 1990; Godvik et al. 2009). We use the results of these studies to study the movements between the “feeding ground” which is used when red deer are active at night and a “resting ground” which is used when red deer are inactive during the day. To identify movement phases (Fig. 3), we used the dispersal approach outlined by Bunnefeld et al. (2011) and Börger and Fryxell (2012) as opposed to the migratory approach used by Papworth et al. (2012). This change overcomes the need for an individual to return to the point of origin by instead fitting a movement model to the outward and return journey separately (Fig. 3). Two dispersal models were fitted, one describing the movement from the resting ground to the feeding ground (the “outward journey”) and one for the journey from the feeding ground back to the resting ground (the “return journey”). Each model analysed a 12-h time period in order to identify the expected movements at dawn or dusk and the stationary period on either side of a movement when deer are either feeding or resting. The 12-h time periods lasted between midday and midnight to detect the expected peak of activity at dusk and dawn. The outward and return journeys were modelled using a logistic model,

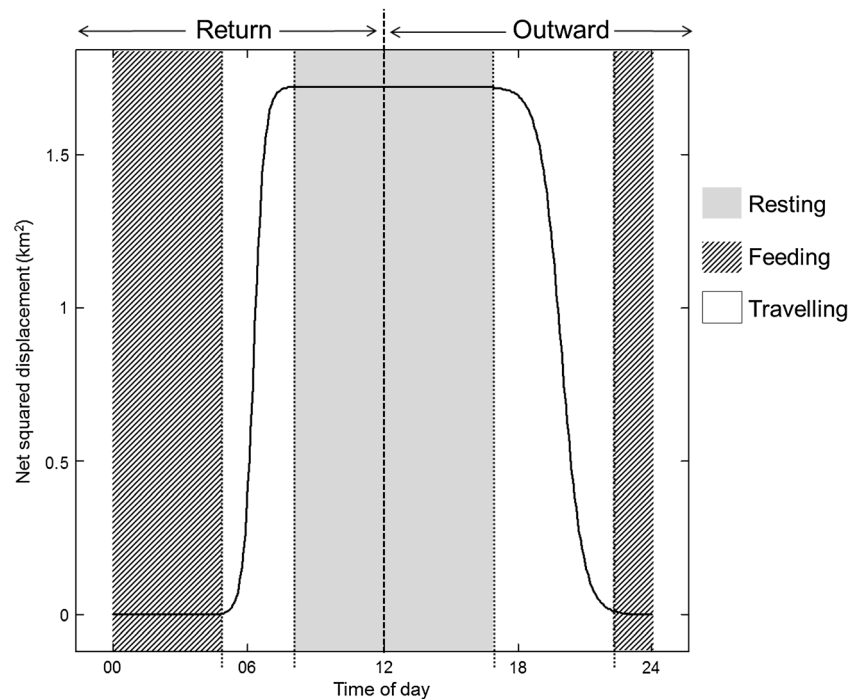
equivalent of a dispersal strategy used in Bunnefeld et al. (2011) and Börger and Fryxell (2012).

$$\text{NSD} = \frac{\delta}{1 + \exp\left(\frac{\theta - t}{\varphi}\right)} \quad (1)$$

where NSD is the net-squared displacement, δ is the asymptotic height (in square kilometers), θ is the timing (in minutes) at which the movement reaches half its asymptotic height, φ models the timing (in minutes) elapsed between reaching $\frac{1}{2}$ and $\sim\frac{3}{4}$ of the asymptote and t is the number of minutes since trip start.

The dispersal strategy was also compared to alternative movement models of home range, nomadism and a null model, as described in Börger and Fryxell (2012) and Singh et al. (2012). Model fit was evaluated using the concordance criterion (CC), which ranges between -1 and 1 , where a CC value <0 indicates lack of fit and higher CC values indicate improved fit (Huang et al. 2009; Singh et al. 2012). Individual red deer and trips were added as random effects to account for the fact that movement data were nested within individuals and that there were multiple trips by the same individual. We tested whether the asymptote (δ), timing (θ) and duration (φ) differed between January, February and March by adding month as a fixed effect. Different combinations of fixed effects

Fig. 3 The theoretical daily movement patterns of a central place forager showing the variation in net displacement over a 24-h time period (solid black line). Our study divides this movement into two segments, the outward journey (right) and the return journey (left). The results of Eq. 1 are used to estimate the feeding (diagonal lines) and resting (shaded grey) times based on when a red deer returns to or leaves the feeding/resting ground



were modelled with the random effects to determine the best model structure, indicated by the CC value. Once the best random effects structure had been determined, movement parameters were generated for the North and South study sites using month as a fixed effect to determine whether movements were influenced by the differing hours of sunlight during the study period. The analysis was performed using R version 2.15.0 (R Development Core Team 2012). Movement trajectories and NSD were calculated using the package adehabitat (Calenge 2006). The data was then modelled using nonlinear mixed effect models in the statistical package nlme (Pinheiro et al. 2012). The results of the model provided estimates for the distance, timing and duration of movements.

Utilisation distribution

The results of the movement models for outward and return journeys were used to divide the daily movements into either feeding or resting (Online Resource 2), using the start and end time of journeys as per Eqs. 2 and 3 and Fig. 3

$$J_s = S + (\theta - 2\varphi) \tag{2}$$

$$J_e = S + (\theta + 2\varphi) \tag{3}$$

where J_s is the time that the outward/return journey starts, J_e is the time the outward/return journey ends, S is the starting time for the data, θ is the time that the outward/return journey reaches half its asymptotic height and φ is the duration (in minutes) elapsed between reaching $\frac{1}{2}$ and $\sim\frac{3}{4}$ of the asymptote of the outward/return journey.

Separate UD were calculated for feeding and resting behaviour using the biased-random bridge (BRB) method (Benhamou and Cornélias 2010; Benhamou 2011). All 12 individuals met the minimum number of 200 locations recommended for UD analysis (Millspaugh et al. 2006; Benhamou and Cornélias 2010). The diffusion coefficient was calculated using the function BRB.D (Benhamou 2011) in the package adehabitatHR (Calenge 2006). Once the UD had been calculated, the area of use at the 50 and 95 % isopleths was calculated using the function kernel.area in adehabitatHR (Calenge 2006). The UD for deer in each study area was combined and the mean taken to compare between the North and South study areas. Once the UD had been computed, a further test was performed to understand how the travelling speed of an individual was correlated to the proportion of open habitats in an individual’s UD. The average speed during the travelling phase (Fig. 3) was calculated and the open habitats included were “arable land” and “pastures”. The correlation was estimated using the Pearson’s product–moment correlation coefficient in R version 2.15.0 (R Development Core Team 2012).

Resource utilisation function

The shapefile containing the UD for each individual was loaded into ArcMap together with the ground cover map for the region. Any points with a UD >95 were excluded; therefore, only grid squares with a 95 % probability of use would be analysed. The dominant habitat for each 25 m×25 m grid cell was extracted using Spatial Join in the geoprocessing tool

reference. The package *ruf*, version 1.5.2 (Handcock 2012), was used to analyse the UD. The log of (100-UD) was used as the response variable to give a normal distribution (Kertson and Marzluff 2010; Papworth et al. 2012). The explanatory variable used was the habitat type. The range and smoothness parameters were estimated by the model using a Matern correlation function (Marzluff et al. 2004; Millspaugh et al. 2006). The mean smoothness for the feeding dataset was 0.64 and 0.90 for the resting dataset. The mean range was 38.31 m for the feeding dataset and 27.10 m for the resting dataset. The standardised coefficient was calculated as this allows the comparison of the relative influence of resources on animal use, whereas the unstandardised coefficient was used to map predicted use of resources (Marzluff et al. 2004). The RUF for each deer was combined and the mean calculated for each study area in order to compare RUFs according to landscape structure. The means were calculated using the function “par.avg” in the R package “MuMIn” (Barton 2013), which is based on model averaging theory by Burnham and Anderson (2002), in order to average the means and standard errors of the RUF model outputs.

Results

Movement patterns

The best fitting model for the movement patterns of all red deer was the dispersal model (Online Resource 3), for both outward and return journeys, using a random effects structure that included trip nested within an individual, and these varied with the fixed effects of month for the asymptote (δ), timing (θ) and duration (φ).

Red deer in the South travelled further than deer in the North on both outward and return journeys (Fig. 4, Online Resource 4), with a number of trips ($n=27$ of 170) in excess of 2 km for the South, compared with just three trips (of 111) exceeding 2 km in the North. Red deer in both regions travelled further on the outward journey compared to the return journey, although this difference was greater in the South, with an average difference of 0.48 km compared to the North with an average difference of 0.18 km. The timing of the outward journey was generally later by 60 min in the South, and the return journey was on average 40 min earlier compared with that in the North. The duration of outward journeys was fairly similar in both regions (125 min) despite deer travelling further in the South. A noticeable difference was that the return journey took 30 min longer in the North compared to that in the South (summary in Fig. 4, Online Resource 4). The average speed whilst travelling had a significant positive correlation with the proportion of open habitat within an individual's UD ($r=0.764$, $n=12$, $P=0.004$), with

the average speed increasing as the proportion of open habitat increases (Fig. 5).

Red deer exhibited different responses in the two study sites with the timing of their outward and return journeys in relation to sunrise and sunset (Table 1). In January, red deer in both regions left the resting place after sunset and returned before sunrise. However, in February, they exhibited differing behaviours, with red deer in the North leaving the resting place before sunset in contrast to the South which left after sunset. Red deer in both regions returned before sunrise in February though. In March, red deer altered their strategies again. Red deer in the North still left the resting place before sunset, but now returned after sunrise. Red deer in the South also left the resting place before sunset but continued to return to the resting place before sunrise.

Utilisation distribution

The average UD for red deer in the North was 1.03 km² whilst feeding and 0.33 km² whilst resting. The average UD for red deer in the South was more than twice as large, with an average of 2.46 km² whilst feeding and 1.31 km² whilst resting. For all individuals, the area utilised whilst feeding was larger than the area utilised whilst resting (Online Resource 5 and 6).

Resource utilisation function

Arable land was the only habitat to be avoided during resting in both study sites (Online Resource 7, Fig. 6). Red deer in the North selected for clear-felled forest and younger forest during resting. The pattern of selection in the South is less clear; however, the selection appears to be higher for forested habitats. The habitats selected for whilst feeding varied across the two study areas. High variation between deer leads to wide error bars; thus, there was no statistically clear pattern. However, red deer in the North showed higher selection for clear-felled areas and to a less degree for pastures and coniferous forest more than 15 m high. To illustrate the cause of the variation with an example, the majority of deer selected for clear-felled habitats in the North, whereas one individual (ID 2167) strongly avoided these habitats and instead selected for pastures (Online Resource 7). Red deer in the South showed some selection for arable land and pastures during feeding but, in contrast to the North, an avoidance of clear-felled areas.

Discussion

Landscape structure and the relative availability of different habitat components in the landscape influenced the daily movement patterns of red deer between feeding and resting locations and the utilisation of these areas. The NSD

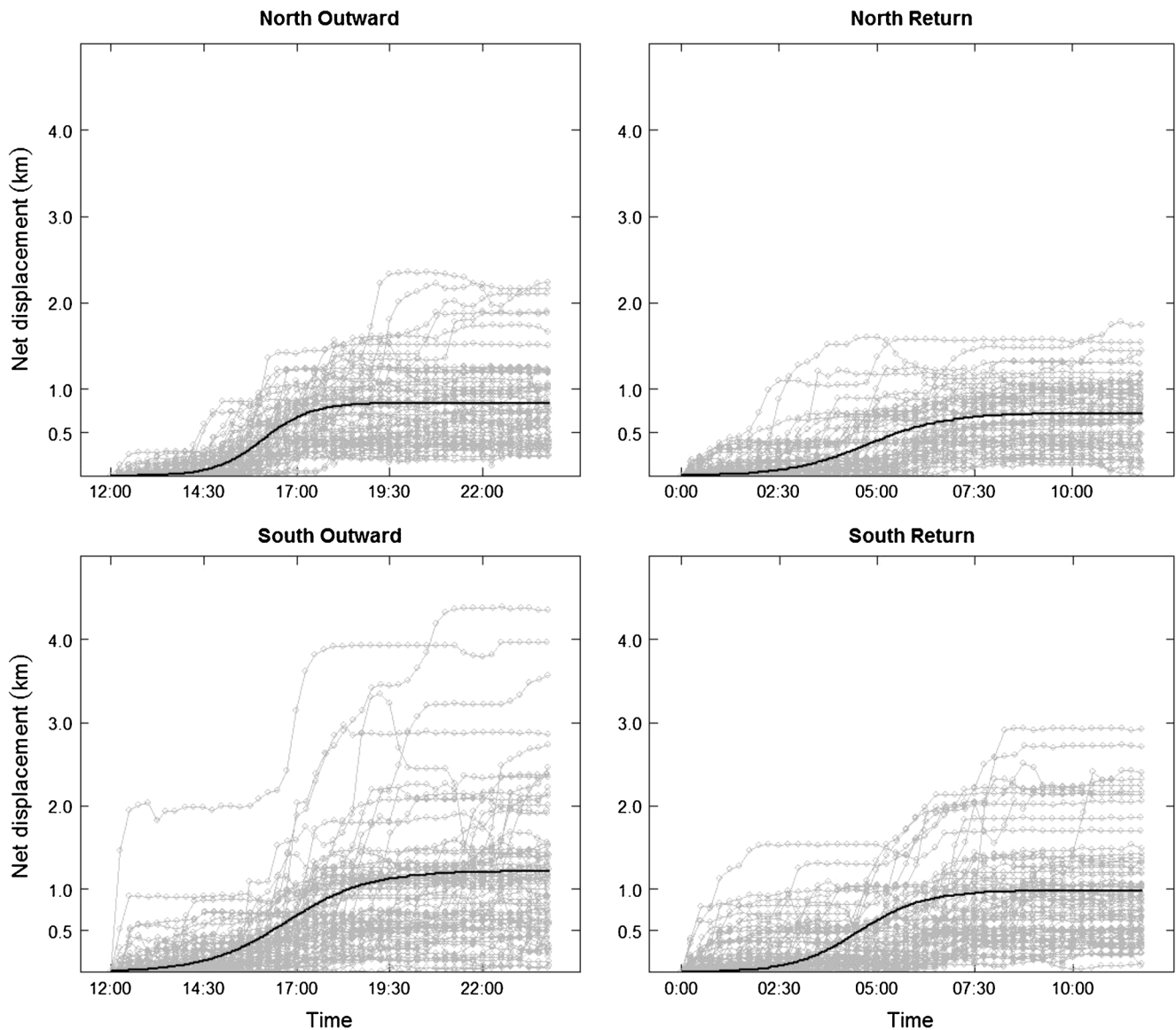


Fig. 4 Outward and return journeys for the North and the South. Trips are shown as *grey points with connecting lines* and the modelled output as a *solid black line*. The outward journey is the movement from the resting ground to the feeding ground and the time period of tracking is from

midday to midnight. The return journey is the movement from the feeding ground to the resting ground and the time period of tracking is from midnight to midday

movement model revealed that the distance travelled between the feeding and resting locations is greater in the South (fragmented, dominated by agriculture) than that in the North (mostly covered by forest); however, the duration of the journey was longer in the North, particularly for the return journey from the feeding to the resting areas. The UD identified regional differences in the area utilised for both feeding and resting. All red deer in the South had larger UDs than red deer in the North, and in some instances, the area utilised was five times larger in the South compared to that in the North. In both study sites, habitats selected whilst resting showed a general trend of preference for coniferous forest, younger forest and clear-felled areas and an avoidance of arable land and pastures. The overall habitat selection patterns of red deer

in both of our study regions show a functional response in habitat selection (Myrsterud and Ims 1998), as reported in previous studies of ungulates (Massé and Côté 2009; Godvik et al. 2009; Bjørneraas et al. 2012). However, we also found differences in habitat selection between the southern and northern areas. Red deer increased selection for coniferous forest as the availability of open habitats increased in the South, whereas in the North, there was increased selection for open habitats as the availability of forest increased. This indicates that the landscape structure impacts habitat selection patterns of red deer in Sweden. These patterns of selection are also influenced by the daily activity rhythms of individuals, as feeding patterns took place in open but exposed habitats whereas resting patterns were in forested and sheltered

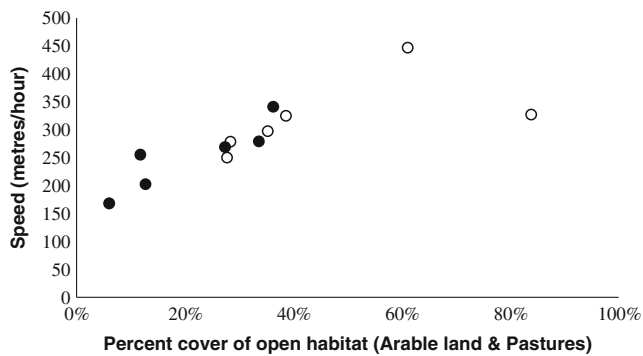


Fig. 5 Travelling speed in relation to percentage cover of open land correlation ($R^2=0.58$). Travelling speed is the average speed in metres per hour during “travelling” phases, i.e. the time period during which red deer are moving to or from the resting/feeding areas. Percentage cover of open land is the proportion of arable land and pastures contained within an individual’s UD. *Solid black points* are red deer in the North and *white points* are red deer in the South

habitats. Therefore, although we have not directly measured costs, our results indicate that red deer in southern Sweden experience a trade-off between food and cover (Myrsterud and Østbye 1999; Godvik et al. 2009).

Red deer in the South show a general trend of selection for most forest types whilst resting, in a landscape dominated by agriculture. Although the forest stands provide cover, they provide little in the way of available forage (Myrsterud and Østbye 1999), which may result in higher levels of bark stripping as observed in previous studies (Månsson and Jarnemo 2013). Coniferous forests >15 m were also selected whilst feeding, alongside open, exposed habitats of arable land and pastures. This segregation of habitat selection clearly indicates a trade-off between using sheltered habitats during the day and foraging habitats at night. Red deer in the North had higher levels of selection for clear-felled forest and younger forest whilst resting. These habitats are a form of human-induced succession, allowing new plant species to colonise the ground and field layer, thus increasing the supply of forage and cover for ungulates (Kuiters et al. 1996; Bergquist et al. 1999). Red deer in the North also had higher levels of selection for clear-felled forests during feeding. Therefore, it appears that red deer in the North use clear-felled forests for both

food and cover, meaning that they experience less of a trade-off compared with the South.

The differing patterns of habitat selection and the trade-off between food and cover are supported by the movement patterns of red deer. Red deer in both regions appear to exhibit movement patterns that are influenced by disturbance. In regions with little or no disturbance, red deer are active during the day and night (Clutton-Brock et al. 1982; Kamler et al. 2007), whereas disturbance causes shifts in activity patterns to night (Georgii 1981; Pépin et al. 2009), as observed in this study. However, the activity patterns varied in the two regions and the need for cover may explain the differences between the North and the South. In our study, the distance travelled by red deer in the South was greater but completed over a shorter duration. Arable land and pastures may be perceived as open, risky habitats (Myrsterud and Østbye 1999); therefore, red deer in the South do not leave the shelter of the forest until after sunset and return to the forest before sunrise, thus using darkness as a form of cover whilst in these open habitats. Movement theory reviewed by Fahrig (2007) indicates that animals moving through risky or low-resource habitats have straighter movement paths, therefore minimising the time spent there, and that spatial aggregation of habitats would favour shorter movement distances. This theory is supported by our results as red deer with a higher proportion of open habitats in their UD had higher travelling speeds. The greater distances travelled by deer in the South also suggest that the habitats that provide food and shelter are segregated in the landscape. In contrast, red deer in the North had shorter movements, suggesting that the habitats that provide food and shelter are more aggregated in the landscape. Red deer movements in the North had a longer duration despite the shorter distances, indicating that they are moving through less risky habitats which may also provide foraging opportunities between the resting and feeding areas. Therefore, the trade-off between food and cover may be lower in the North, which is why the timing of movement is not so strictly aligned to the hours of darkness.

The space use patterns of red deer may also provide insights into the structure of habitats selected by red deer. The average UD was at least twice as large in the South compared

Table 1 Comparison of the timing that a red deer leaves the resting area (outward) or returns to the resting area (return) in relation to the changing hours of daylight

	North		South		North		South	
	Sunset	Outward	Sunset	Outward	Sunrise	Return	Sunrise	Return
Jan	15:14	16:46	15:55	17:07	08:37	08:15	08:32	06:58
Feb	16:28	15:51	17:00	18:00	07:37	07:06	07:43	07:18
Mar	17:37	16:09	18:00	16:42	06:20	07:32	06:36	05:42

The sunset and sunrise times indicate the mean sunset or sunrise during the relevant month. The timing of outward and return journeys is calculated from Eqs. 2 and 3, using the model outputs in Online Resource 4

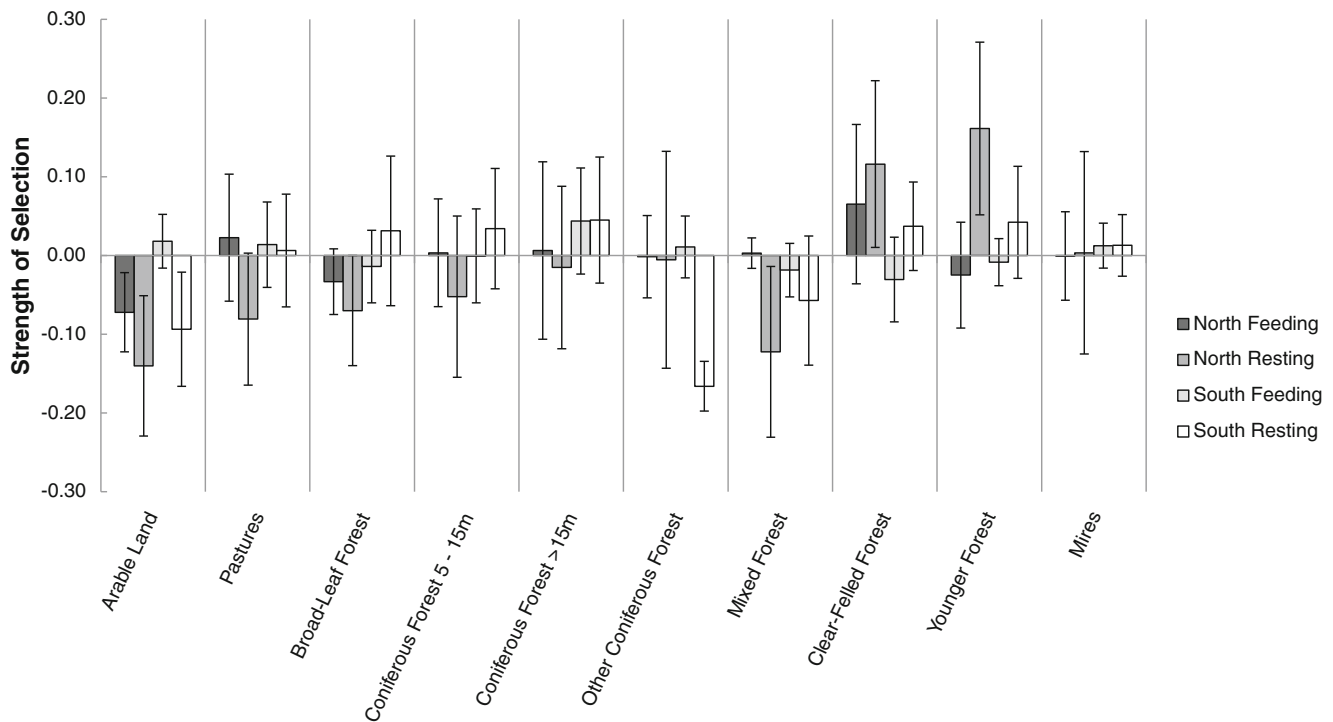


Fig. 6 Standardised resource utilisation function (RUF) coefficients by habitat type, for feeding and resting, in the North and the South study sites. Positive RUF values indicate that use of a resource is greater than expected based on availability, and negative RUF values indicate that use

of a resource is less than expected based on availability. The *errors bars* show the standard errors of the averaging process (i.e. from averaging the means and standard errors of the RUF model outputs)

to that in the North. The intra-specific variation in the size of home ranges is still poorly understood (Anderson et al. 2005; Saïd and Servanty 2005), with explanations that include seasonal variation, density, availability of resources and shelter, (Tufto et al. 1996; Kjellander et al. 2004; Anderson et al. 2005; Börger et al. 2006). However, a more common body of theory is that space use is more strongly related to resource availability (Tufto et al. 1996; Anderson et al. 2005). This is supported by theoretical work that suggests that as resources become scarce across the landscape, or distributed over a wider area, organisms may need to operate at larger spatial scales in order to meet their demands (O'Neill et al. 1988). The larger UD in the South supports this theory, along with the habitat selection and movement patterns reported above. The habitats that provide food and cover are more segregated in the South, meaning that red deer need to operate at larger spatial scales to meet their demands. In contrast, habitats that provide food and cover are more aggregated in the North, so red deer are able to operate at smaller spatial scales and hence utilise a smaller portion of the landscape. These differing movement patterns show how changes in the landscape structure influence the movement and feeding behaviour of red deer in the two study regions. The intra-specific variation in space use may also interact with deer density. Unfortunately, no figures of local density are available for our study sites, but the harvest data indicates that the density is generally higher in

the North. Therefore, we cannot rule out a potential effect of density; however, the relationship between home range size and density (inferred from hunting bag statistics) is variable (Online Resource 5). Therefore, we doubt that the effect of density is of high relevance compared to the parameters included in our study.

This application of the methodological framework proposed by Papworth et al. (2012) appears to have been appropriate in correctly identifying several behavioural characteristics of red deer reported in previous studies. The results of the UD and RUF confirm that during winter, red deer are feeding (active) at night and resting (inactive) during the day (Georgii 1981; Green and Bear 1990; Godvik et al. 2009), as shown through the larger UD at night and the use of open, feeding habitats during this time compared to the use of more closed habitats that provide shelter during the day. Separating these behaviours is important for habitat selection studies (Mysterud and Ims 1998; Godvik et al. 2009), and the combination of methods used in this study has provided an objective and accurate means of differentiating between these movement states and linking them to space use and habitat selection. Through the unified framework applied in this study, one is able to gain a better understanding of how, why, when and where an animal moves, thus advancing the movement ecology paradigm (Nathan et al. 2008). The generality of the approach means that this unified framework

can be applied to the increasing number of species able to carry GPS devices.

Our study has shown how various methods in movement ecology can be combined to further our understanding of the behavioural responses of red deer in landscapes with contrasting habitats and level of fragmentation. The variation influenced by differences in the landscape structure is reflected in the functional responses of red deer and their space use patterns. This knowledge has important management implications, as the trade-off between food and cover may influence the levels of bark stripping (Månsson and Jarnemo 2013). Management actions that improve the spatial distribution and availability of resources in the landscape may contribute towards alleviating this human–wildlife conflict, potentially avoiding the need to reduce deer numbers. The results from studies such as these are vital for furthering our ecological understanding of species adaptation to human-induced changes in the landscape and adapting management strategies to these ecological responses.

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