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

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Summary

1. 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. Methods in movement ecology that identify the movement characteristics, utilisation distribution (UD) and habitat selection patterns of a species can provide important insights into species response to changes in the landscape.
2. This study combines all three fields of movement, utilisation distribution and habitat selection into a single approach. The framework is applied to red deer (*Cervus elaphus*) in southern Sweden, in order to understand how landscape structure influences their movement and feeding patterns. Red deer movements are compared between two regions, one being dominated by a fragmented agriculture-forest mosaic and the other by managed homogenous forest.
3. Red deer in the agriculture dominated landscape had larger UDs for feeding and resting than deer in the forest dominated area; they moved larger distances between feeding and resting, left cover later in the day (timing) but used a similar duration for their movements, suggesting that they move faster between resting and feeding locations.
4. Red deer in both regions showed a functional response in habitat selection, selecting for coniferous forest as the availability of open habitats increased in the agricultural landscape, whereas in the forested landscape, there was increased selection for open habitats as the availability of forest increased. The habitat selection patterns indicate that red deer experience 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.

5. 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 GPS devices.

Key-words: animal movement, biased-random bridge, landscape ecology, net squared displacement, nonlinear mixed models, resource utilisation function, spatial ecology, 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 & 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'Neil 1988; Mysterud & Ims 1998, Rivrud, Loe & Mysterud 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 to range over larger areas when resource availability is low (Tufto, Andersen & Linnell 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 indicate that the relative use of a habitat changes according to its availability, a process known as functional responses in habitat selection (Mysterud & 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 its 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, Guinness, & Albon 1982; Pepin, Morellet & Goulard 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, Loe & Mysterud 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 & 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 it's 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 change, 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 that 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, Anderson, & Putman 2010; Månsson & 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. Skåne (N55°65E13°50) is the southernmost county (hereafter South) and Södermanland- Östergötland (N58°75E16°40) is in the south-east (hereafter North). The dominant habitat type in the South is agricultural land covering 45% of the landscape while 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 800mm (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 10cm (SMHI 2012). In the North, the mean annual temperature is 5.5°C with mean annual precipitation of 787mm (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 35cm (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 as individuals harvested per 1000ha is approximately double the amount harvested in the South study site (Månsson & Jarnemo 2013).

Methods

Movement Data

Red deer hinds were fitted with a Global positioning system (GPS) collar (Vectronic Aerospace PRO Light 3D) and a plastic ear tag for identification. Only adult hinds (at least two 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 6 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 minutes once a week. The GPS data was screened using the method outlined by Bjørneraas *et al.* (2010; Appendix S1). Hunting in both regions caused deer to travel several kilometres before returning back to the study site a few days later (Jarnemo & Wikenros 2013). Hunting dates were provided for both regions therefore the data was further screened to remove movements on these days. 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 Ver 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 25m x 25m. 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 used the approach outlined by Papworth et al. (2012) linking net-squared displacement to identify movement, resting and feeding phases, utilisation distribution to quantify the area used during the three phases and the resource utilisation function to analyse habitat selection (Fig 1).

To identify movement phases (Fig 2), we used the dispersal approach outlined by Bunnefeld *et al.* (2011) and Börger & Fryxell (2012). 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 a resting ground (the "return journey"). Each model analysed a 12 hour 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 hour 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 & Fryxell (2012).

$$\mathrm{NSD} = \frac{\delta}{1+\exp\left(\frac{\theta-t}{\varphi}\right)} \qquad \text{Eqn1}$$

where δ is the asymptotic height (in km^2), θ is the timing (in minutes) at which the movement reaches half its asymptotic height, φ models the timing (in minutes) elapsed between reaching ½ and ~¾ 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 & 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, Mang & Yang 2009; Singh *et al.* 2012). Individual red deer and trip 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 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 software (R Development Core Team 2012, Version 2.15.0). 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 (UD)

The results of the movement models for outward and return journeys were used to divide the daily movements into either feeding or resting (Table S1), using the start and end time of journeys as per equations 2 and 3 and Fig 3

$J_s = S + (\theta - 2\varphi)$ Eqn2

$J_e = S + (\theta + 2\varphi)$ Eqn3

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 ½ and ~¾ of the asymptote of the outward/return journey.

Separate UDs were calculated for feeding and resting behaviour using the biased-random bridge (BRB) method (Benhamou & Cornélis 2010; Benhamou 2011). All 12 individuals met the minimum number of 200 locations recommended for UD analysis (Millspaugh *et al.* 2006; Benhamou & Cornélis 2010). The diffusion coefficient was calculated using the function BRB.D (Benhamou 2011) in the package Adehabitat (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 function in Adehabitat (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 2) 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 (R Development Core Team 2012, Version 2.15.0).

Resource Utilisation Function (RUF)

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 25m x 25m 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 (Kerston & 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 38.31m for the feeding dataset and 27.10m 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 is 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.

Results

Movement Patterns

The best fitting model for the movement patterns of all red deer was the dispersal model (Fig S1), for both outward and return journeys, using a random effects structure that included trip nested within individual and that 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 3, Table 1), with a number of trips (n=27 of 170) in excess of 2km for the South, compared with just three trips (of 111) exceeding 2km 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 0.48km compared to the North with an average difference of 0.18km. The timing of the outward journey was generally later by 60 minutes in the South and the return journey was on average 40 minutes earlier compared with the North. The duration of outward journeys were fairly similar in both regions (125 minutes) despite deer travelling further in the South. A noticeable difference was that the return journey took 30 minutes longer in the North compared to the South (summary in Fig 3, Table 1). 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 4).

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 2). In January, red deer in both regions left the resting place after sunset and returned before sunrise. However, in February they exhibited differing behaviour 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 (UD)

The average UD for red deer in the North was 1.03km^2 while feeding and 0.33km^2 while resting. The average UD for red deer in the South was at least twice as large, with an average of 2.46km^2 while feeding and 1.31km^2 while resting. For all individuals, the area utilised while feeding was larger than the area utilised while resting (Table S2).

Resource Utilisation Function (RUF)

Younger forest during resting was the only habitat to be selected for in both study sites, whilst arable land was avoided in both areas during resting (Table S3, Fig 5). The habitats selected for while feeding varied across the two study areas. Red deer in the North strongly selected for clear-felled areas and had lower selection for pastures and coniferous forest >15m. Red deer in the South showed some selection for arable land and pastures, but in contrast to the North, an avoidance of clear-felled areas. While resting, red deer in both study sites selected for clear-felled areas and younger forest, however, the South also selected for broad-leaf forest, coniferous forest 5 - 15m and coniferous forest >15m.

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 movement model revealed that the distance travelled between the feeding and resting locations is greater in the South (fragmented, dominated by agriculture) than 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 the North. In both study sites, habitats selected while 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 (Mysterud & Ims 1998), as reported in previous studies of ungulates (Godvik *et al.* 2009; Massé & Côté 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 habitats. Therefore, red deer in southern Sweden experience a trade-off between food and cover (Mysterud & 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 (Mysterud & Østbye, 1999), which may result in higher levels of bark stripping as observed in previous studies (Månsson & Jarnemo, 2012). Coniferous forests >15m 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 plants species to colonise the ground and field layer thus increasing the supply of forage and cover for ungulates (Kuiters, Mohren, & Van Wieren 1996; Bergquist, Örlander & Nilsson 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, Guinness & Albon 1982; Kamler, Jedrzejewska, & Jedrzejewski 2007), whereas disturbance causes shifts in activity patterns to night (Georgii 1981; Pepin, Morellet & Goulard 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 (Mysterud & 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 suggests that the habitats that provide food and shelter are segregated in the landscape. In contrast, red deer in the North had shorter movements over a longer duration, suggesting that they are moving through less risky habitats and that the habitats that provide food and shelter are more aggregated in the landscape. Therefore, the trade-off between food and cover may be lower in the North, which is why the timing of movements 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 to the North. The intra-specific variation in the size of home ranges is still poorly understood (Anderson et al. 2005, Said & Servanty 2005), with explanations that include seasonal variation, availability of resources and shelter, (Tufto, Andersen & Linnell 1996; Anderson et al. 2005; Börger *et al.* 2006). However, theory 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 UDs 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 methodology framework 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 & Bear 1990; Godvik et al. 2009). Separating these behaviours is important for habitat selection studies (Mysterud & 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 outstanding 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 & Jarnemo 2012). 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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Figures

Figure 1 - Methodology Framework for the analysis of red deer movement patterns and feeding decisions

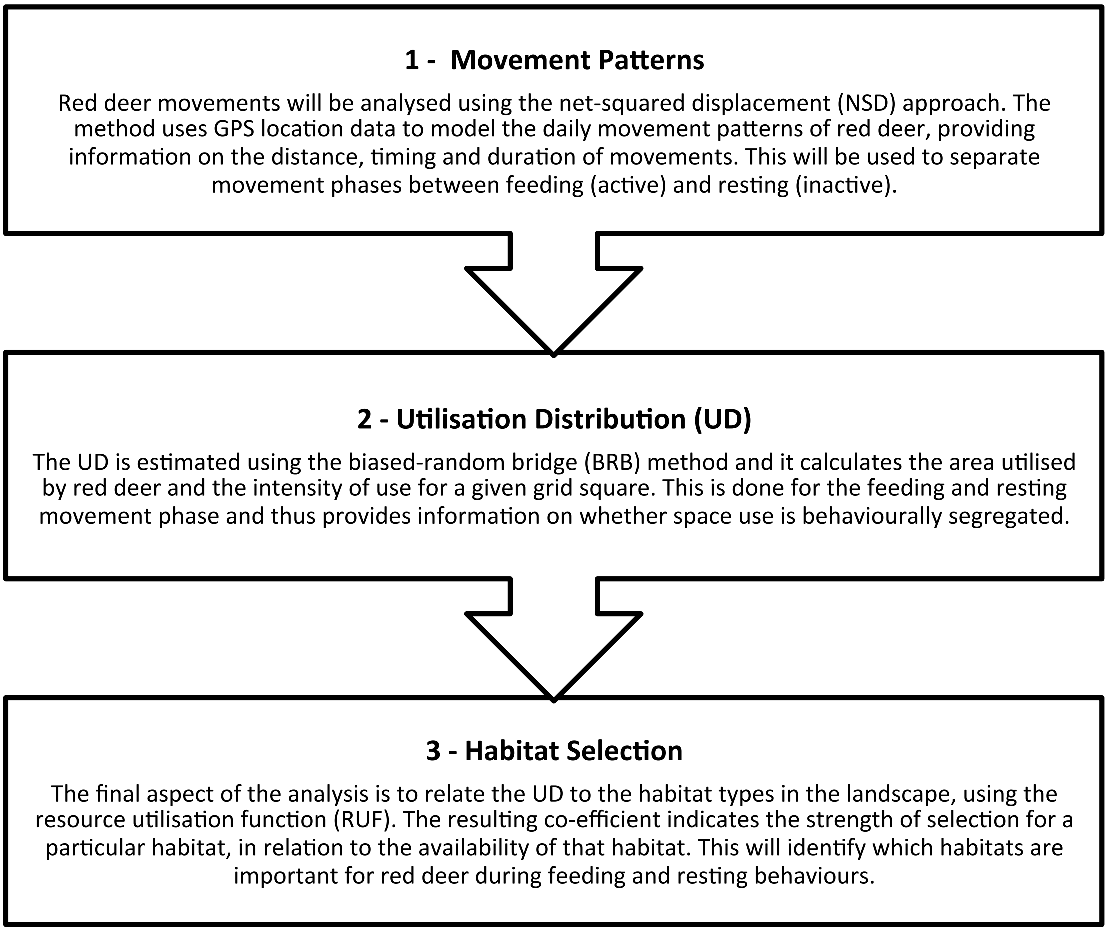
Figure 2 – The theoretical daily movement patterns of a central place forager showing the variation in net displacement over a 24 hour time period (solid black line). Our study divides this movement into two segments, the outward journey (right) and the return journey (left). The results of Eqn1 are 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.

Figure 3 - 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

Figure 4 – 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, white points are red deer in the South.

Figure 5 - 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 error bars indicate the 95% confidence limits.

Figure 1



1 - Movement Patterns

Red deer movements will be analysed using the net-squared displacement (NSD) approach. The method uses GPS location data to model the daily movement patterns of red deer, providing information on the distance, timing and duration of movements. This will be used to separate movement phases between feeding (active) and resting (inactive).

2 - Utilisation Distribution (UD)

The UD is estimated using the biased-random bridge (BRB) method and it calculates the area utilised by red deer and the intensity of use for a given grid square. This is done for the feeding and resting movement phase and thus provides information on whether space use is behaviourally segregated.

3 - Habitat Selection

The final aspect of the analysis is to relate the UD to the habitat types in the landscape, using the resource utilisation function (RUF). The resulting co-efficient indicates the strength of selection for a particular habitat, in relation to the availability of that habitat. This will identify which habitats are important for red deer during feeding and resting behaviours.

606 **Figure 2**

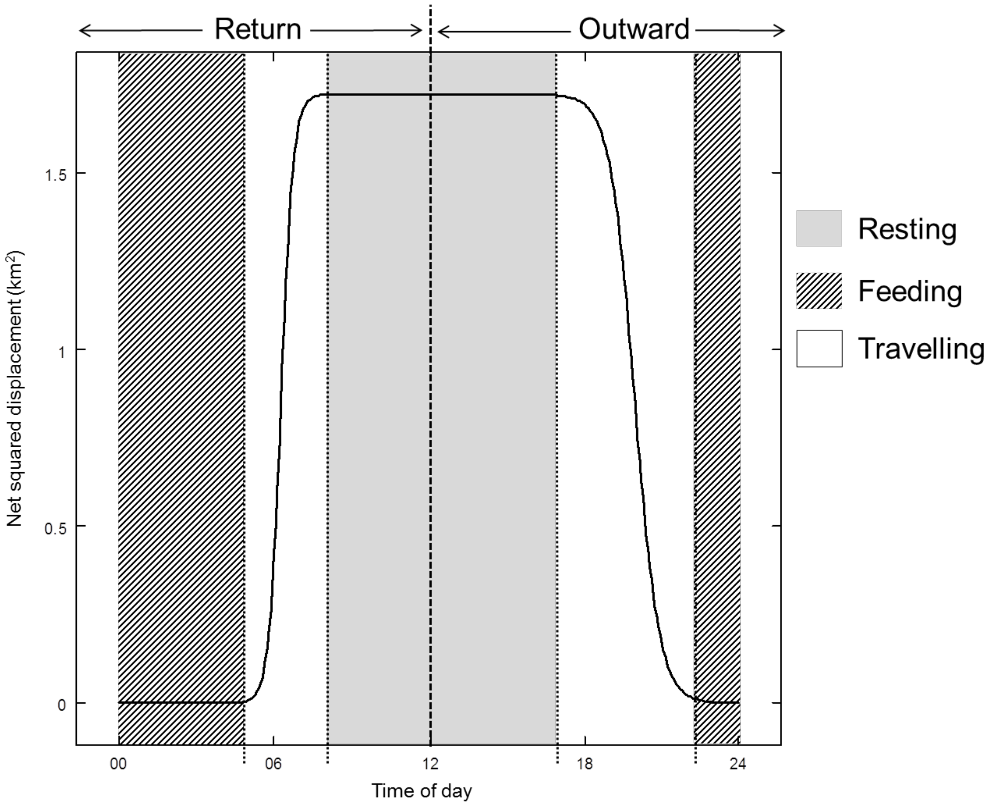


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Figure 3

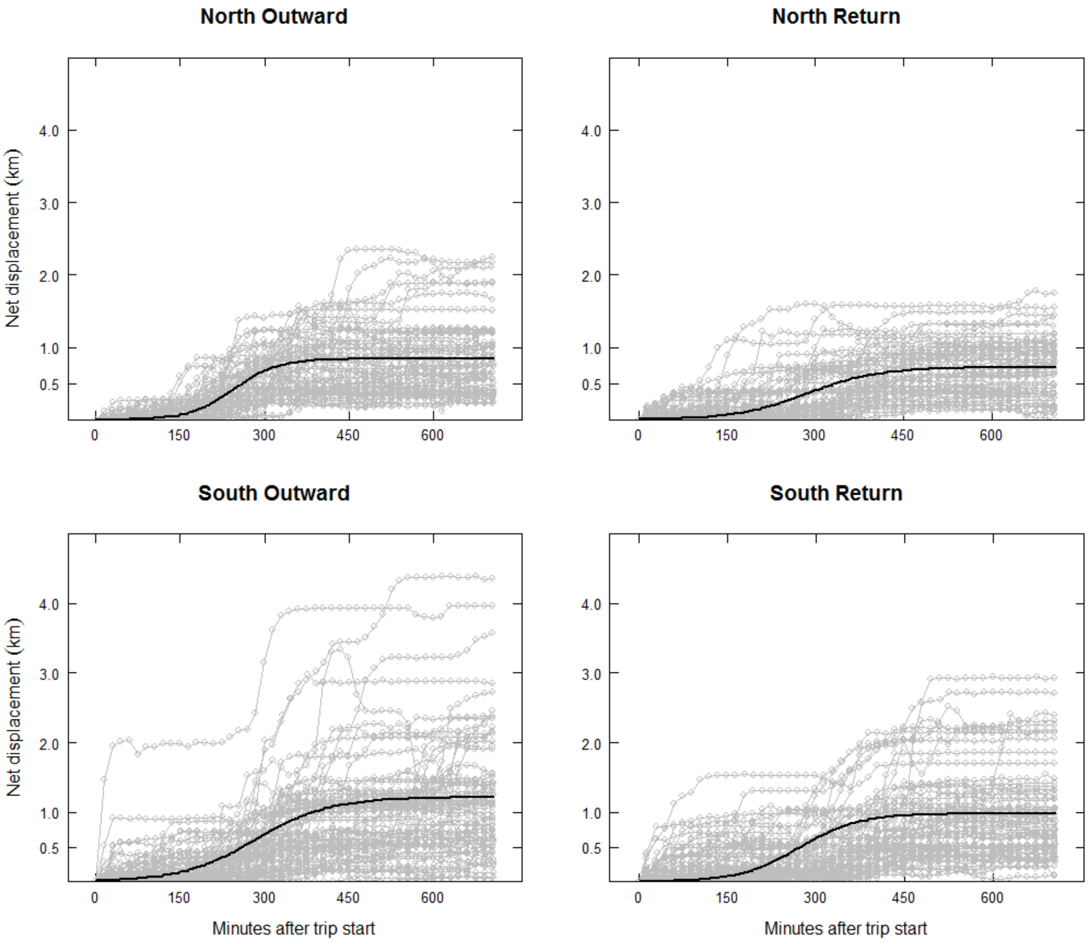

North Outward
North Return
South Outward
South Return
Net displacement (km)
4.0
3.0
2.0
1.0
0.5
0
150
300
450
600
Minutes after trip start

Figure 4

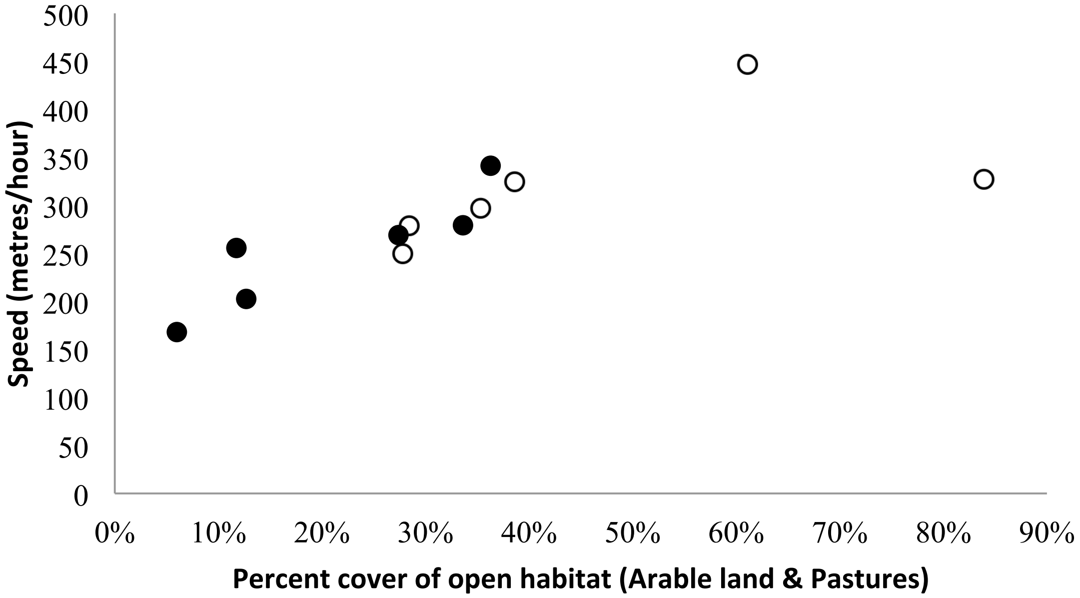
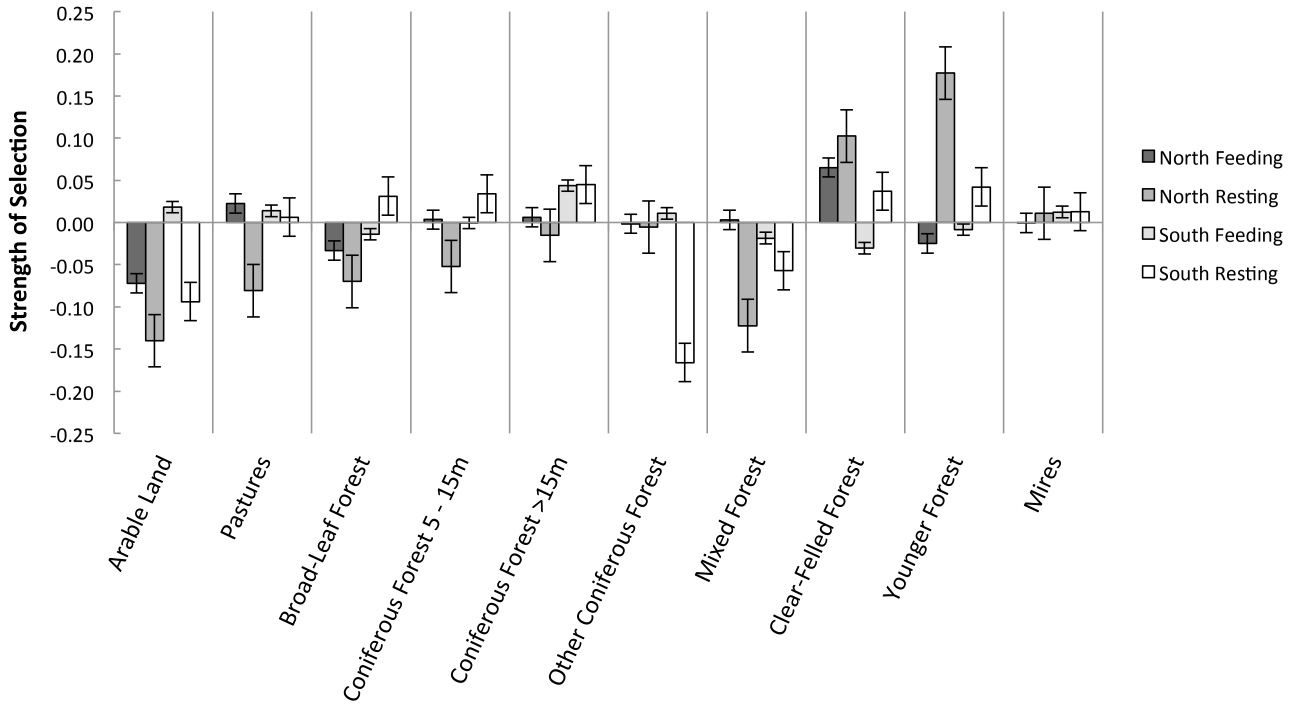

500
450
400
350
300
250
200
150
100
50
0
Speed (metres/hour)
0%
10%
20%
30%
40%
50%
60%
70%
80%
90%
Percent cover of open habitat (Arable land & Pastures)

Figure 5


Strength of Selection
0.25
0.20
0.15
0.10
0.05
0.00
-0.05
-0.10
-0.15
-0.20
-0.25
Arable Land
Pastures
Broad-Leaf Forest
Coniferous Forest 5 - 15m
Coniferous Forest >15m
Other Coniferous Forest
Mixed Forest
Clear-Felled Forest
Younger Forest
Mires
North Feeding
North Resting
South Feeding
South Resting

Tables

Table 1 Net Squared Displacement (NSD) model outputs (see Eqn 1) for outward and return journeys in the North (top) and South (bottom) with 95% confidence intervals (C.I.), where δ is the asymptotic height (converted to km), θ is the timing (in minutes) at which the movement reaches half its asymptotic height and φ is the timing (in minutes) elapsed between reaching ½ and ~¾ of the asymptote

North	**Month**	**Outward**		**Return**	
		Model Result	**C.I. (+/-)**	**Model Result**	**C.I. (+/-)**
Asymptote (δ) (km)	**January**	1.16	0.87	0.91	0.67
	February	1.06	0.93	0.87	0.71
	March	0.93	0.92	0.81	0.70
	Average	1.05	0.91	0.87	0.70
Timing (θ) (minutes)	**January**	346.4	59.0	413.8	80.9
	February	297.4	65.9	346.7	93.6
	March	307.3	65.1	356.8	92.6
	Average	317.0	63.3	372.4	89.1
Duration (φ) (minutes)	**January**	29.9	22.0	40.8	26.0
	February	33.2	27.0	39.7	31.5
	March	28.9	27.4	47.8	31.9
	Average	30.7	25.5	42.8	29.8
South					
Asymptote (δ) (km)	**January**	1.51	1.24	1.29	0.85
	February	2.04	1.53	1.23	1.03
	March	1.42	1.55	1.01	1.06
	Average	1.66	1.44	1.18	0.98
Timing (θ) (minutes)	**January**	366.6	57.6	359.2	48.6
	February	439.8	87.6	367.9	72.9
	March	347.7	91.1	273.9	79.2
	Average	384.7	78.8	333.7	66.9
Duration (φ) (minutes)	**January**	29.5	14.5	29.4	12.0
	February	39.6	21.8	35.1	17.8
	March	32.5	24.1	34.5	20.2
	Average	33.9	20.1	33.0	16.7

Table 2 Comparison of 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

Supporting Information

Figure S1 – Concordance Criterion (CC) values for each movement model: HR = Home Range model, Null = Null model, Nomad = Nomadic model, Disp1 = Dispersal model that includes asymptote (δ) as a random effect, Disp2 = Dispersal model that includes asymptote (δ) and timing (θ) as random effects, Disp3 = Dispersal model that includes asymptote (δ), timing (θ) and duration (φ) as random effects.

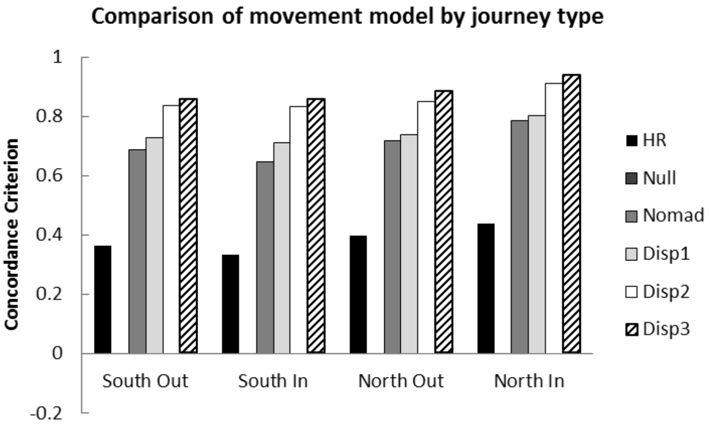


Figure S2 – Utilisation distribution (UD) maps for all red deer in the North (IDs 2122 to 2171) and South (IDs 3152 to 3200). The intensity of use for feeding is indicated by a graduated scale from yellow (low intensity) to red (high intensity). The intensity of use for resting is indicated by a graduated scale from blue (low intensity) to green (high intensity).

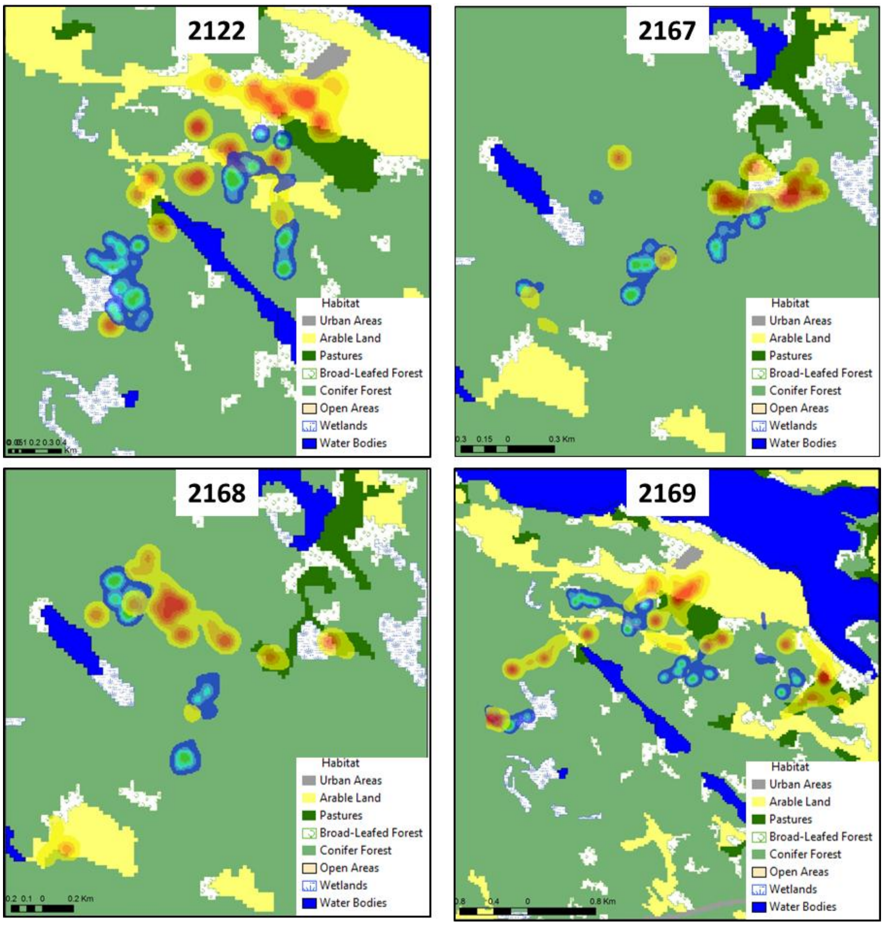


Figure S2 (cont.)

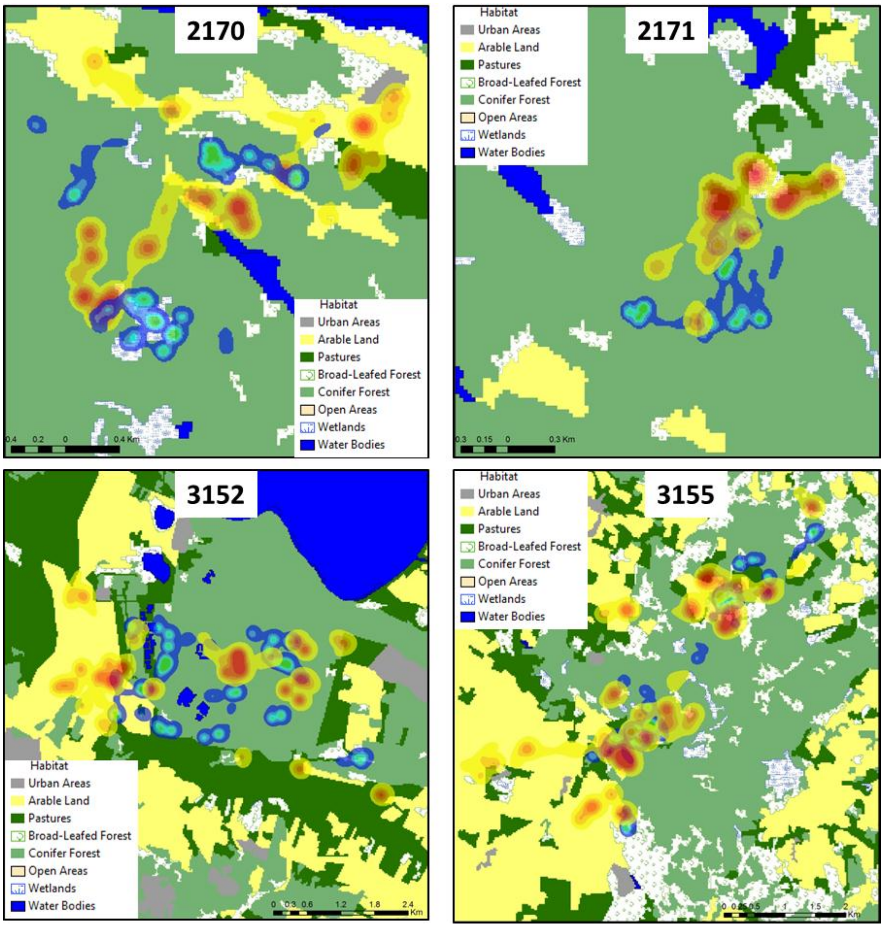


Figure S2 (cont.)

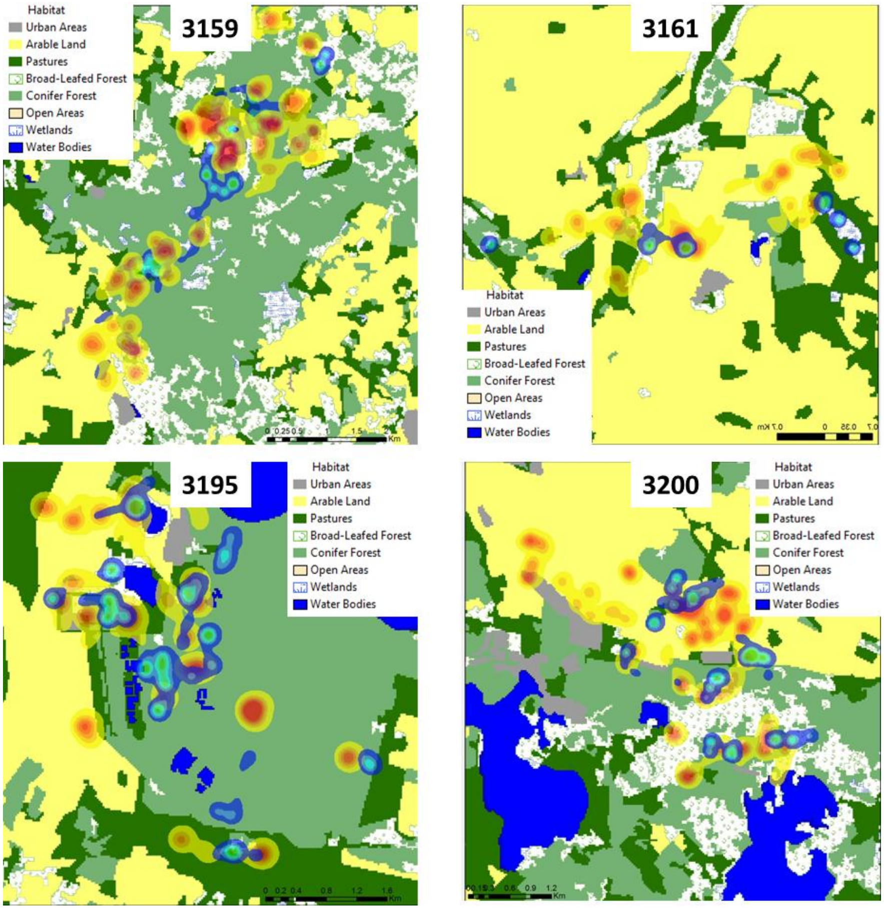


Table S1 Feeding and resting times for red deer used for the analysis of the utilisation distribution (UD)

	Feeding		**Resting**	
	Start	**End**	**Start**	**End**
North January	18:46:12	05:32:12	08:15:24	16:46:36
North February	18:03:48	04:27:18	07:06:06	15:51:00
North March	18:05:06	04:21:12	07:32:24	16:09:30
South January	19:05:36	05:00:24	06:58:00	17:07:36
South February	20:39:00	04:57:42	07:18:06	18:00:36
South March	18:52:42	03:24:54	05:42:54	16:42:42

Table S2 – Utilisation distribution area (in km^2) for the feeding and resting dataset, for each individual at 50% and 95% probability of use in the North (top) and South (bottom)

Region	ID	Feeding		Resting	
		50	95	50	95
North	**2122**	0.24	1.09	0.09	0.44
	2167	0.10	0.65	0.02	0.14
	2168	0.11	0.64	0.03	0.18
	2169	0.42	2.11	0.07	0.41
	2170	0.21	1.22	0.07	0.53
	2171	0.09	0.49	0.03	0.27
South	**3152**	0.42	2.63	0.38	1.77
	3155	0.38	2.10	0.20	1.30
	3159	0.53	3.27	0.29	1.78
	3161	0.30	2.07	0.06	0.56
	3195	0.36	2.20	0.16	1.36
	3200	0.50	2.46	0.15	1.07

Table S3 – Resource utilisation function results for Feeding (top) and Resting (middle) for each individual sorted for the North (2122 to 2171) and the South (3152 to 3200), with the coding for each habitat (bottom) and the number of deer utilising each habitat

ID	30	32	40	41	43	44	45	46	47	48	49	54	55	71	72
2122	-0.05	-0.02	0.01			-0.00	0.05		0.05			0.06	-0.10		
2167		0.15			-0.02	0.04	-0.16					-0.11	0.07	0.03	
2168	-0.08	-0.05			-0.08	-0.06	0.10	0.05	-0.02			0.15	-0.03	0.01	
2169	-0.03	0.02	-0.06		-0.03	0.01	0.06		0.05	0.00		0.09	-0.05		-0.03
2170	-0.12	0.02	-0.05		-0.05	0.09	0.02		0.02			0.16	-0.07		-0.02
2171		0.02			0.02	-0.06	-0.04	-0.01				0.03	0.01	0.06	-0.05
3152	0.04	-0.06	0.00			0.03	0.02			-0.00			-0.02		
3155	0.00	0.01	-0.01			-0.03	0.10	0.04		-0.02	-0.03	-0.06	0.01		0.00
3159	0.02	0.03	0.03			-0.01	-0.01	-0.02		-0.01		-0.05	-0.00		0.02
3161	0.02	0.05	0.01			-0.06							-0.01		
3195	-0.00	-0.02	-0.05			0.09	0.10			-0.04		-0.05	-0.02		
3200	0.03	0.08	-0.08	0.01		-0.01	-0.04			-0.04	0.02	0.04	-0.00		

ID	30	32	40	41	43	44	45	46	47	48	49	54	55	71	72
2122	-0.16	-0.05	-0.09			0.04	0.08	0.02	0.03			0.14			-0.02
2167		-0.05					-0.05					0.10	0.09	-0.09	
2168	-0.21				-0.17		-0.04		-0.04	-0.17		0.23	0.40		
2169	-0.04		-0.05			-0.02	-0.11	0.01	0.06	-0.07		0.07	0.18		-0.04
2170	-0.15				-0.13	-0.09	0.05	-0.10	0.12			-0.05	0.17		0.18
2171		-0.14				-0.15	-0.02	0.14				0.13	0.04		
3152	-0.14	-0.07	-0.04			0.12	0.10			-0.00		0.05	-0.00		
3155	-0.15	0.06	0.13			0.02	0.10	-0.17		-0.13		0.04	0.10		0.01
3159	-0.16	0.06	0.13			0.03	0.09	-0.16		-0.16		0.05	0.12		-0.01
3161	-0.00	-0.07	0.03	0.14		-0.07	-0.02						-0.05		0.04
3195	-0.11	-0.01	-0.06			0.11	0.07			-0.10		0.09	0.01		
3200	-0.00	0.07	-0.08	-0.00		0.00	-0.06			-0.02	0.06	-0.04	0.07		

Code	Habitat Type	Feeding	Resting
30	Arable land	10	10
32	Pastures	12	9
40	Broad-leaf forest not on mires	9	8
41	Broad-leaf forest on mires	1	2
43	Coniferous forest on lichen	5	2
44	Coniferous forest 5-15 m	12	10
45	Coniferous forest >15 m	11	12
46	Coniferous forest on mires	4	6
47	Conif. forest on open bedrock	4	4
48	Mixed forest not on mires	6	7
49	Mixed forest on mires	2	1
54	Clear-felled areas	10	11
55	Younger forest	12	11
71	Wet mires	3	1
72	Other mires	5	6

Appendix S1 – GPS Data Screening

Approximately 105,000 GPS data points were collected from the South and 110,000 from the North during the course of the study period. Two types of error can occur which are missing location fixes and location error (Lewis *et al.* 2007). There were 4,907 missing location fixes overall providing a fix success rate of 97.7%. Previous studies have shown that missing location fixes are usually systematic and not random (Frair *et al.* 2004). The success rate of location fixes may be influenced by habitat features such as canopy height and cover (DeCesare *et al.* 2005; Di Orio *et al.* 2003) or temporal features such as the time of year (Edenius 1997). This habitat-induced data loss may result in biased habitat selection models potentially leading to type II errors of failing to detect significant model coefficients (Nielson *et al.* 2009). Despite the potential bias of missing locations, the issue has been largely ignored (Frair *et al.* 2004), resulting in data thinning as the points are removed from the datasets. However, the methods proposed for this study do not require data thinning therefore preventing some of the bias caused by missing locations. Nonlinear NSD models estimate missing locations by extrapolating between known locations for the movement study (Papworth *et al.* 2012) and the BRB method can interpolate between recorded locations (Benhamou 2011).

The second type of error in GPS data is location error. A location error is the difference between an animal’s true location and the position recorded by a GPS collar (Bjørneraas *et al.* 2010). Location errors may result in the misclassification of habitats used in resource selection functions (Visscher 2006) and may introduce bias into movement data (Hurford 2009). There are two measures of accuracy for a GPS location; these are the number of satellites and the satellite geometry. A two-dimensional (2D) fix is when three satellites are recorded simultaneously and a three-dimensional (3D) fix is four or more satellites (Lewis *et al.* 2007). Satellite geometry is measured by the dilution of precision (DOP) and a low DOP value represents higher accuracy due to improved triangulation by the satellites (Langley 1999). The GPS data collected during the study period has a high degree of accuracy as over 95% of records have 3D fixes and over 97% of records have a DOP of less than 10 metres. Some screening methods suggest the removal of 2D fixes (D'Eon *et al.* 2002; Lewis *et al.* 2007) or points with a high DOP (D'Eon & Delparte 2005), or a combination of the two (Lewis *et al.* 2007). These screening methods could result in the loss of between 1,200 to 16,000 data points for this study, depending on the method used. Instead, a recently adapted method, which incorporates the movement characteristics of an animal, will be used to screen the data for location errors. The method outlined in Bjørneraas *et al.* (2010) uses two steps to identify potential location errors. The first step identifies locations farther away than a pre-set distance from surrounding points and the second step identifies erroneous spikes in turning angle and speed. Based on knowledge of red deer movement and behaviour in the study areas, the following parameters were used in the screening model:

Δ = 10km
μ = 5km
α = 1.5 km/hour
θ = 0.97

where Δ is a large, predefined distance that the animal is unlikely to travel within the maximum sampling interval, μ is a large, predefined distance that the animal is not likely to have travelled, α is a predefined threshold for speed and θ is a predefined threshold for turning angle (Bjørneraas *et al.* 2010). The screening method was done using the open-source statistical software R (R Development Core Team 2012, Version 2.15.0) and it requires the package Adehabitat (Calenge 2006). This method detected a total of 98 location errors that were removed from the dataset.

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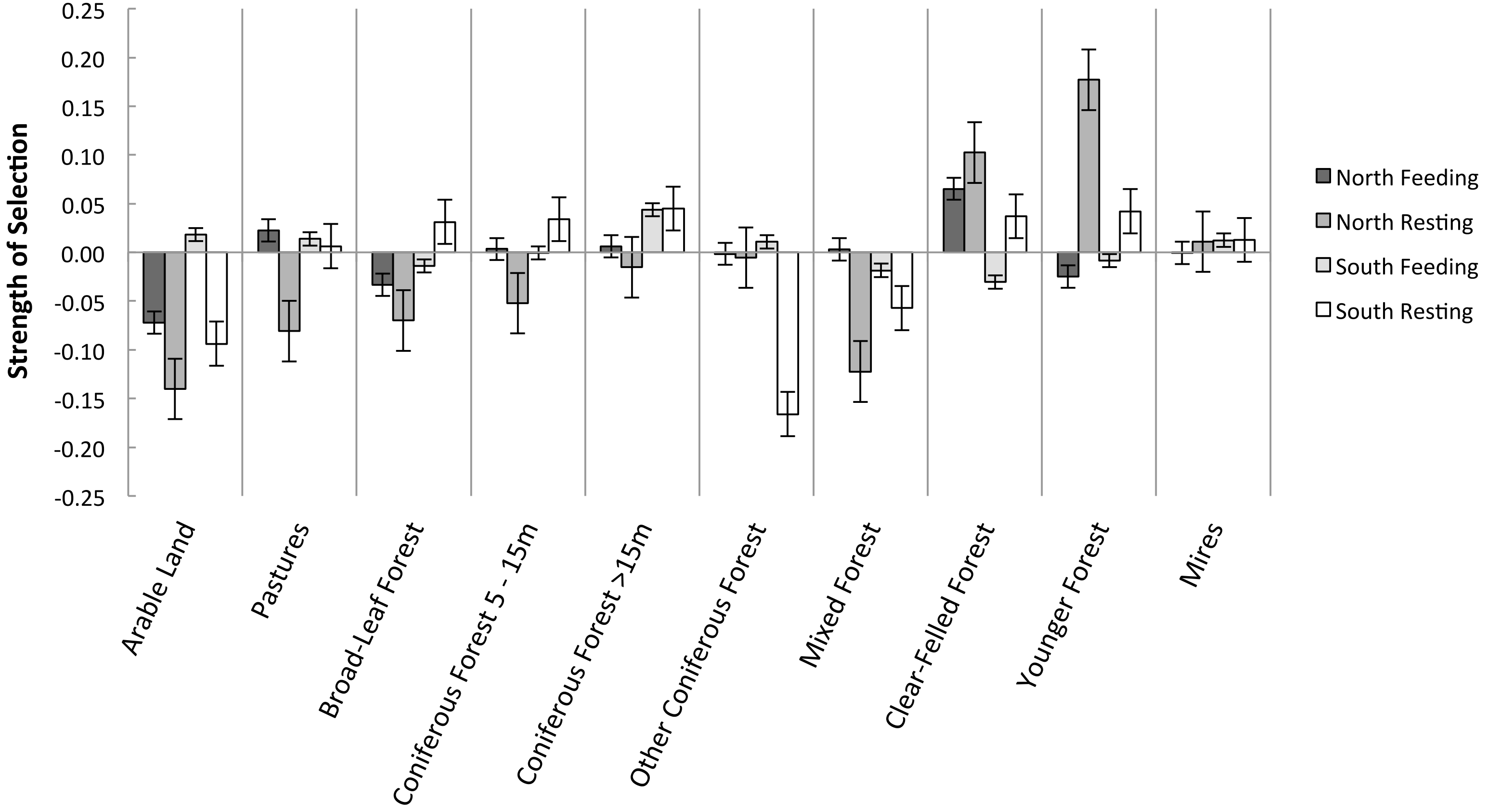
Figure 5


Strength of Selection
0.25
0.20
0.15
0.10
0.05
0.00
-0.05
-0.10
-0.15
-0.20
-0.25
Arable Land
Pastures
Broad-Leaf Forest
Coniferous Forest 5 - 15m
Coniferous Forest >15m
Other Coniferous Forest
Mixed Forest
Clear-Felled Forest
Younger Forest
Mires
North Feeding
North Resting
South Feeding
South Resting

Tables

Table 1 Net Squared Displacement (NSD) model outputs (see Eqn 1) for outw return journeys in the North (top) and South (bottom) with 95% confidence in where δ is the asymptotic height (converted to km), θ is the timing (in minutes the movement reaches half its asymptotic height and φ is the timing (in minut between reaching ½ and ~¾ of the asymptote

North	**Month**	**Outward**		**Return**	
		Model Result	**C.I. (+/-)**	**Model Result**	**C.I**
Asymptote (δ) (km)	**January**	1.16	0.87	0.91	
	February	1.06	0.93	0.87	
	March	0.93	0.92	0.81	
	Average	1.05	0.91	0.87	
Timing (θ) (minutes)	**January**	346.4	59.0	413.8	
	February	297.4	65.9	346.7	
	March	307.3	65.1	356.8	
	Average	317.0	63.3	372.4	
Duration (φ) (minutes)	**January**	29.9	22.0	40.8	
	February	33.2	27.0	39.7	
	March	28.9	27.4	47.8	
	Average	30.7	25.5	42.8	
South					
Asymptote (δ) (km)	**January**	1.51	1.24	1.29	
	February	2.04	1.53	1.23	
	March	1.42	1.55	1.01	
	Average	1.66	1.44	1.18	
Timing (θ) (minutes)	**January**	366.6	57.6	359.2	
	February	439.8	87.6	367.9	
	March	347.7	91.1	273.9	
	Average	384.7	78.8	333.7	
Duration (φ) (minutes)	**January**	29.5	14.5	29.4	
	February	39.6	21.8	35.1	
	March	32.5	24.1	34.5	
	Average	33.9	20.1	33.0	

Table 2 Comparison of 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

Supporting Information

Figure S1 – Concordance Criterion (CC) values for each movement model: HR = Home Range model, Null = Null model, Nomad = Nomadic model, Disp1 = Dispersal model that includes asymptote (δ) as a random effect, Disp2 = Dispersal model that includes asymptote (δ) and timing (θ) as random effects, Disp3 = Dispersal model that includes asymptote (δ), timing (θ) and duration (φ) as random effects.

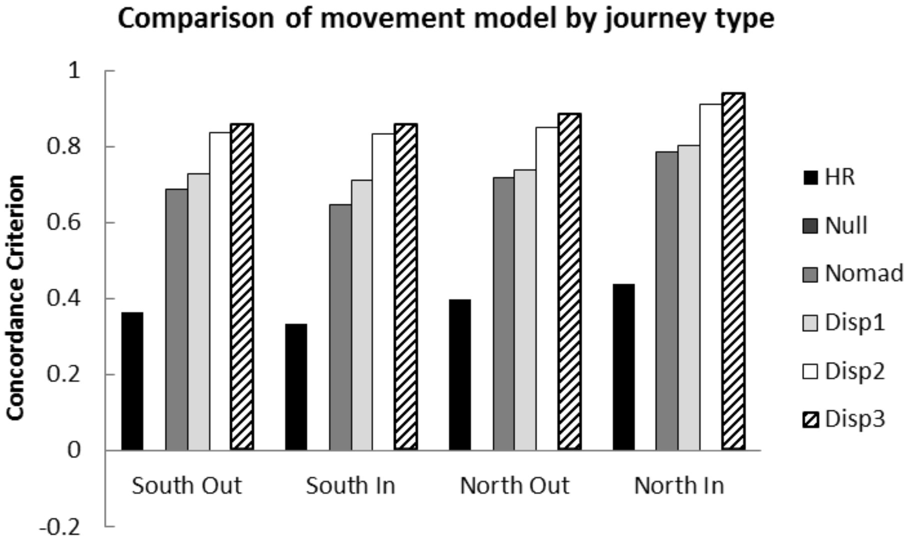


Figure S2 – Utilisation distribution (UD) maps for all red deer in the North (IDs 2122 to 2171) and South (IDs 3152 to 3200). The intensity of use for feeding is indicated by a graduated scale from yellow (low intensity) to red (high intensity). The intensity of use for resting is indicated by a graduated scale from blue (low intensity) to green (high intensity).

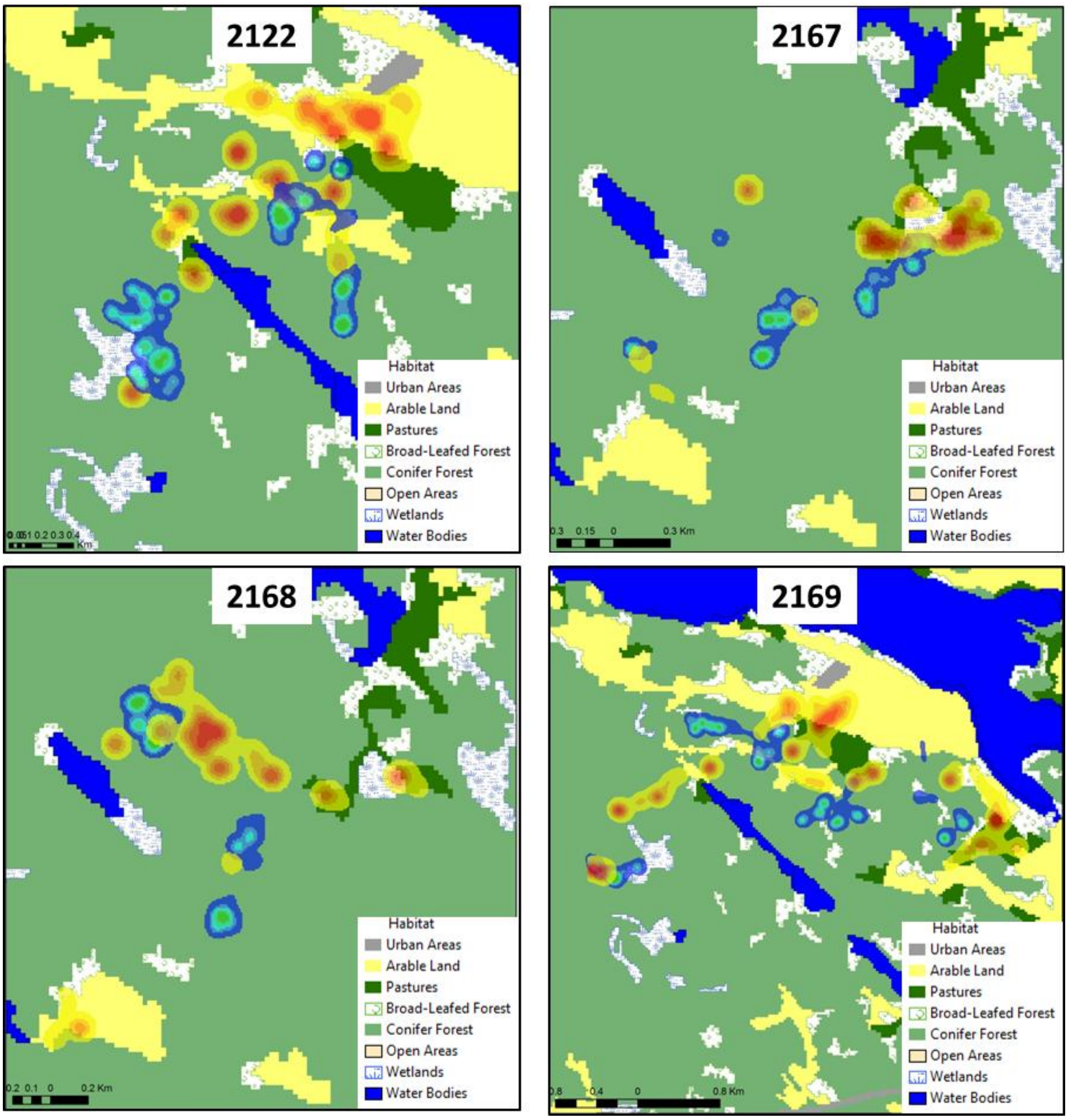


Figure S2 (cont.)

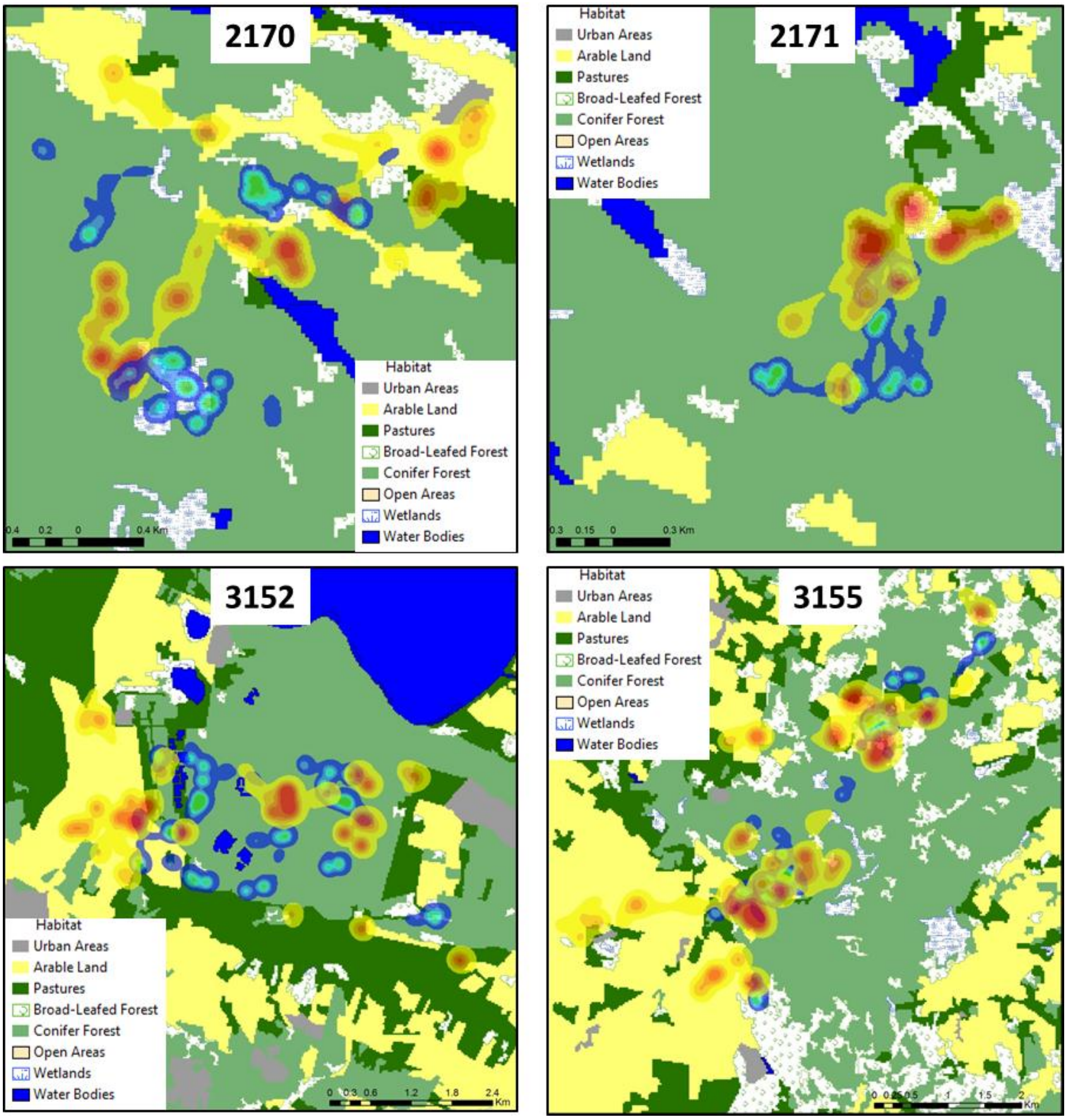


Figure S2 (cont.)

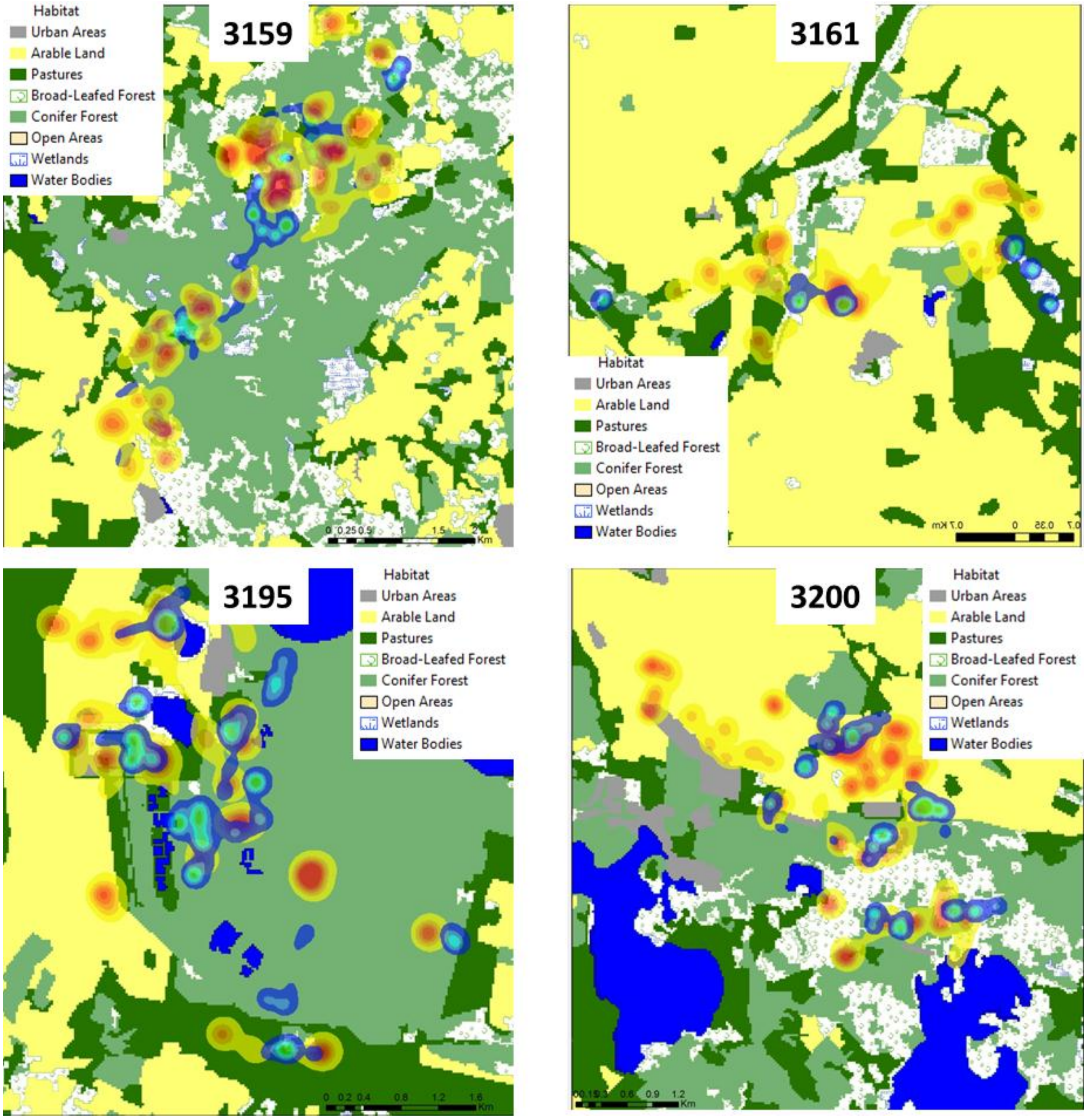


Table S1 Feeding and resting times for red deer used for the analysis of the utilisation distribution (UD)

	Feeding		**Resting**	
	Start	**End**	**Start**	**End**
North January	18:46:12	05:32:12	08:15:24	16:46:36
North February	18:03:48	04:27:18	07:06:06	15:51:00
North March	18:05:06	04:21:12	07:32:24	16:09:30
South January	19:05:36	05:00:24	06:58:00	17:07:36
South February	20:39:00	04:57:42	07:18:06	18:00:36
South March	18:52:42	03:24:54	05:42:54	16:42:42

Table S2 – Utilisation distribution area (in km^2) for the feeding and resting dataset, for each individual at 50% and 95% probability of use in the North (top) and South (bottom)

Region	ID	Feeding		Resting	
		50	**95**	**50**	**95**
North	**2122**	0.24	1.09	0.09	0.44
	2167	0.10	0.65	0.02	0.14
	2168	0.11	0.64	0.03	0.18
	2169	0.42	2.11	0.07	0.41
	2170	0.21	1.22	0.07	0.53
	2171	0.09	0.49	0.03	0.27
South	**3152**	0.42	2.63	0.38	1.77
	3155	0.38	2.10	0.20	1.30
	3159	0.53	3.27	0.29	1.78
	3161	0.30	2.07	0.06	0.56
	3195	0.36	2.20	0.16	1.36
	3200	0.50	2.46	0.15	1.07

Table S3 – Resource utilisation function results for Feeding (top) and Resting (middle) for each individual sorted for the North (2122 to 2171) and the South (3152 to 3200), with the coding for each habitat (bottom) and the number of deer utilising each habitat

ID	30	32	40	41	43	44	45	46	47	48	49	54	55	71	72
2122	-0.05	-0.02	0.01			-0.00	0.05		0.05			0.06	-0.10		
2167		0.15			-0.02	0.04	-0.16					-0.11	0.07	0.03	
2168	-0.08	-0.05			-0.08	-0.06	0.10	0.05	-0.02			0.15	-0.03	0.01	
2169	-0.03	0.02	-0.06		-0.03	0.01	0.06		0.05	0.00		0.09	-0.05		-0.03
2170	-0.12	0.02	-0.05		-0.05	0.09	0.02		0.02			0.16	-0.07		-0.02
2171		0.02			0.02	-0.06	-0.04	-0.01				0.03	0.01	0.06	-0.05
3152	0.04	-0.06	0.00			0.03	0.02			-0.00			-0.02		
3155	0.00	0.01	-0.01			-0.03	0.10	0.04		-0.02	-0.03	-0.06	0.01		0.00
3159	0.02	0.03	0.03			-0.01	-0.01	-0.02		-0.01		-0.05	-0.00		0.02
3161	0.02	0.05	0.01			-0.06							-0.01		
3195	-0.00	-0.02	-0.05			0.09	0.10			-0.04		-0.05	-0.02		
3200	0.03	0.08	-0.08	0.01		-0.01	-0.04			-0.04	0.02	0.04	-0.00		

ID	30	32	40	41	43	44	45	46	47	48	49	54	55	71	72
2122	-0.16	-0.05	-0.09			0.04	0.08	0.02	0.03			0.14			-0.02
2167		-0.05					-0.05					0.10	0.09	-0.09	
2168	-0.21				-0.17		-0.04		-0.04	-0.17		0.23	0.40		
2169	-0.04		-0.05			-0.02	-0.11	0.01	0.06	-0.07		0.07	0.18		-0.04
2170	-0.15				-0.13	-0.09	0.05	-0.10	0.12			-0.05	0.17		0.18
2171		-0.14				-0.15	-0.02	0.14				0.13	0.04		
3152	-0.14	-0.07	-0.04			0.12	0.10			-0.00		0.05	-0.00		
3155	-0.15	0.06	0.13			0.02	0.10	-0.17		-0.13		0.04	0.10		0.01
3159	-0.16	0.06	0.13			0.03	0.09	-0.16		-0.16		0.05	0.12		-0.01
3161	-0.00	-0.07	0.03	0.14		-0.07	-0.02						-0.05		0.04
3195	-0.11	-0.01	-0.06			0.11	0.07			-0.10		0.09	0.01		
3200	-0.00	0.07	-0.08	-0.00		0.00	-0.06			-0.02	0.06	-0.04	0.07		

Code	**Habitat Type**	**Feeding**	**Resting**
30	Arable land	10	10
32	Pastures	12	9
40	Broad-leaf forest not on mires	9	8
41	Broad-leaf forest on mires	1	2
43	Coniferous forest on lichen	5	2
44	Coniferous forest 5-15 m	12	10
45	Coniferous forest >15 m	11	12
46	Coniferous forest on mires	4	6
47	Conif. forest on open bedrock	4	4
48	Mixed forest not on mires	6	7
49	Mixed forest on mires	2	1
54	Clear-felled areas	10	11
55	Younger forest	12	11
71	Wet mires	3	1
72	Other mires	5	6

Appendix S1 – GPS Data Screening

Approximately 105,000 GPS data points were collected from the South and 110,000 from the North during the course of the study period. Two types of error can occur which are missing location fixes and location error (Lewis *et al.* 2007). There were 4,907 missing location fixes overall providing a fix success rate of 97.7%. Previous studies have shown that missing location fixes are usually systematic and not random (Frair *et al.* 2004). The success rate of location fixes may be influenced by habitat features such as canopy height and cover (DeCesare *et al.* 2005; Di Orio *et al.* 2003) or temporal features such as the time of year (Edenius 1997). This habitat-induced data loss may result in biased habitat selection models potentially leading to type II errors of failing to detect significant model coefficients (Nielson *et al.* 2009). Despite the potential bias of missing locations, the issue has been largely ignored (Frair *et al.* 2004), resulting in data thinning as the points are removed from the datasets. However, the methods proposed for this study do not require data thinning therefore preventing some of the bias caused by missing locations. Nonlinear NSD models estimate missing locations by extrapolating between known locations for the movement study (Papworth *et al.* 2012) and the BRB method can interpolate between recorded locations (Benhamou 2011).

The second type of error in GPS data is location error. A location error is the difference between an animal's true location and the position recorded by a GPS collar (Bjørneraas *et al.* 2010). Location errors may result in the misclassification of habitats used in resource selection functions (Visscher 2006) and may introduce bias into movement data (Hurford 2009). There are two measures of accuracy for a GPS location; these are the number of satellites and the satellite geometry. A two-dimensional (2D) fix is when three satellites are recorded simultaneously and a three-dimensional (3D) fix is four or more satellites (Lewis *et al.* 2007). Satellite geometry is measured by the dilution of precision (DOP) and a low DOP value represents higher accuracy due to improved triangulation by the satellites (Langley 1999). The GPS data collected during the study period has a high degree of accuracy as over 95% of records have 3D fixes and over 97% of records have a DOP of less than 10 metres. Some screening methods suggest the removal of 2D fixes (D'Eon *et al.* 2002; Lewis *et al.* 2007) or points with a high DOP (D'Eon & Delparte 2005), or a combination of the two (Lewis *et al.* 2007). These screening methods could result in the loss of between 1,200 to 16,000 data points for this study, depending on the method used. Instead, a recently adapted method, which incorporates the movement characteristics of an animal, will be used to screen the data for location errors. The method outlined in Bjørneraas *et al.* (2010) uses two steps to identify potential location errors. The first step identifies locations farther away than a pre-set distance from surrounding points and the second step identifies erroneous spikes in turning angle and speed. Based on knowledge of red deer movement and behaviour in the study areas, the following parameters were used in the screening model:

$\Delta = 10\text{km}$
$\mu = 5\text{km}$
$\alpha = 1.5\text{ km/hour}$
$\theta = 0.97$

where Δ is a large, predefined distance that the animal is unlikely to travel within the maximum sampling interval, μ is a large, predefined distance that the animal is not likely to have travelled, α is a predefined threshold for speed and θ is a predefined threshold for turning angle (Bjørneraas *et al.* 2010). The screening method was done using the open-source statistical software R (R Development Core Team 2012, Version 2.15.0) and it requires the package Adehabitat (Calenge 2006). This method detected a total of 98 location errors that were removed from the dataset.

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