

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

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14

15 **Summary**

- 16 1. An area of research that has recently gained more attention is to understand how
17 species respond to environmental change, such as the landscape structure and
18 fragmentation. Movement is crucial to select habitats but the landscape structure
19 influences the movement patterns of animals. Methods in movement ecology that
20 identify the movement characteristics, utilisation distribution (UD) and habitat
21 selection patterns of a species can provide important insights into species response to
22 changes in the landscape.
- 23 2. This study combines all three fields of movement, utilisation distribution and habitat
24 selection into a single approach. The framework is applied to red deer (*Cervus elaphus*)
25 in southern Sweden, in order to understand how landscape structure influences their
26 movement and feeding patterns. Red deer movements are compared between two
27 regions, one being dominated by a fragmented agriculture-forest mosaic and the other
28 by managed homogenous forest.
- 29 3. Red deer in the agriculture dominated landscape had larger UD's for feeding and
30 resting than deer in the forest dominated area; they moved larger distances between
31 feeding and resting, left cover later in the day (timing) but used a similar duration for
32 their movements, suggesting that they move faster between resting and feeding
33 locations.
- 34 4. Red deer in both regions showed a functional response in habitat selection, selecting
35 for coniferous forest as the availability of open habitats increased in the agricultural
36 landscape, whereas in the forested landscape, there was increased selection for open
37 habitats as the availability of forest increased. The habitat selection patterns indicate
38 that red deer experience a trade-off between forage and cover, selecting for habitats
39 that provide shelter during the day and forage by night. However, the level of trade-off,

40 mediated through movement and space use patterns, is influenced by the landscape
41 structure.

42 5. Our approach provides further understanding of the link between individual animal
43 space use and changing landscapes and can be applied to many species able to carry
44 GPS devices.

45

46 **Key-words:** animal movement, biased-random bridge, landscape ecology, net squared
47 displacement, nonlinear mixed models, resource utilisation function, spatial ecology,
48 wildlife management

49

50 **Introduction**

51

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

62

63 Movement ecology provides a number of insights into potential responses to landscape
64 change. Home range studies have shown that roe deer (*Capreolus capreolus*) are required
65 to range over larger areas when resource availability is low (Tufto, Andersen & Linnell
66 1996). Such patterns are also supported by theoretical work that animals moving through a
67 habitat with low resource availability will have straighter and quicker movements, as the
68 animal searches for higher quality habitats (Fahrig 2007). Research into red deer (*Cervus*
69 *elaphus*) habitat selection indicate that the relative use of a habitat changes according to its
70 availability, a process known as functional responses in habitat selection (Mysterud & Ims
71 1998; Godvik *et al.* 2009). Therefore, as seasons or humans modify the proportion of
72 habitats in the landscape and resource availability, one can expect the selection of preferred
73 habitats to increase as its availability decreases. The pattern of selection may also vary
74 with the daily rhythm of feeding and resting, as Godvik *et al.* (2009) show that open

75 habitats are favoured at night when red deer are feeding whilst closed habitats are favoured
76 during the day when red deer are resting, an activity pattern that may be a response to
77 human disturbance (Georgii 1981; Clutton-Brock, Guinness, & Albon 1982; Pepin,
78 Morellet & Goulard 2009). These studies indicate how research into habitat selection and
79 movement characteristics of a species can be important tools for understanding species
80 adaptations to changes in the landscape.

81

82 Recent studies have focused on either large-scale yearly patterns of moose and red deer
83 movement in relation to phenology (Bischof et al. 2012, van Moorter et al. 2013), or on
84 small scale red deer habitat selection that depended on home range estimates and the time
85 of day used as a proxy for feeding and resting phases (Rivrud, Loe & Mysterud 2010).

86 Here we present a study on animal movement that aims to understand how differences in
87 the landscape structure in two study areas (agriculture versus forest dominated) influence
88 the daily movement of a species (the timing, duration and distance). The study uses a
89 unified framework that links movement and habitat selection patterns of a species, thus
90 contributing to advancing the conceptual framework of movement ecology (Nathan et al.
91 2008). Our methodology distinguishes between movement and stationary phases using an
92 objective and model driven approach (Bunnefeld et al. 2011, Börger & Fryxell, 2012), and
93 thus divides an animal's movement between feeding and resting periods, providing results
94 that link to first principals of an animal's internal state and it's interaction with biotic and
95 abiotic factors (Nathan et al. 2008).

96

97 The red deer system in Sweden is an ideal case study, as the species is managed in
98 contrasting landscapes of forest dominated areas to a fragmented mosaic of agriculture
99 with smaller forest patches. The knowledge gained from this study will not only improve

100 our understanding of animal movement in response to landscape and environmental
101 change, but will also contribute to formulating future management plans. This is of
102 particular interest for a species such as the red deer, whose population has increased
103 dramatically in recent decades and that involves different stakeholders with competing
104 objectives; it is a valuable game species (high density desirable) but can cause considerable
105 costs to forestry through browsing damage (low density desirable; Milner et al. 2006;
106 Apollonio, Anderson, & Putman 2010; Månsson & Jarnemo 2013). Combining movement
107 ecology and habitat selection provides a unique opportunity to improve our understanding
108 and assess its effectiveness within a comparable framework of wild red deer occurring in
109 structurally different landscapes.

110

111 Study Site

112

113 This study was undertaken in two regions of southern Sweden. Skåne (N55°65E13°50) is

114 the southernmost county (hereafter South) and Södermanland- Östergötland

115 (N58°75E16°40) is in the south-east (hereafter North). The dominant habitat type in the

116 South is agricultural land covering 45% of the landscape while forests only cover 35%.

117 Norway spruce is the main forest type (38%) followed by broadleaf forests (35%;

118 Skogsdata 2011). In contrast, the North's landscape is mainly covered by forests (55%)

119 and agricultural land is only 20%. Forests in the North are predominately split between

120 Scots Pine (32%), Norway spruce (28%) and Mixed Conifer forests (18%; Skogsdata,

121 2011). The mean annual temperature in the South is 6.5°C with mean annual precipitation

122 of 800mm (WMO normal period 1961 – 1990; SMHI 2012). During the same period, the

123 average number of snow days per year was 40 with a mean max depth of 10cm (SMHI

124 2012). In the North, the mean annual temperature is 5.5°C with mean annual precipitation

125 of 787mm (WMO normal period 1961 – 1990; SMHI 2012). During the same period, the

126 average number of snow days per year was 80 with a mean max depth of 35cm (SMHI

127 2012). The density of red deer in the two study sites are unknown, however harvest data

128 indicates that the density of red deer is higher in the North study site as individuals

129 harvested per 1000ha is approximately double the amount harvested in the South study site

130 (Månsson & Jarnemo 2013).

131

132

133 **Methods**

134

135 *Movement Data*

136 Red deer hinds were fitted with a Global positioning system (GPS) collar (Vectronic

137 Aerospace PRO Light 3D) and a plastic ear tag for identification. Only adult hinds (at least

138 two years old) were fitted with a collar, however the exact age of collared deer is unknown.

139 Handling protocols were examined by the animal ethics committee for central Sweden and

140 fulfilled the ethical requirements for research on wild animals (decisions M258-06 and 50-

141 06). Data is available for 12 red deer, containing 6 individuals from each study area. GPS

142 locations were recorded during the winter months of January, February and March 2008

143 and locations were recorded every 15 minutes once a week. The GPS data was screened

144 using the method outlined by Bjørneraas *et al.* (2010; Appendix S1). Hunting in both

145 regions caused deer to travel several kilometres before returning back to the study site a

146 few days later (Jarnemo & Wikenros 2013). Hunting dates were provided for both regions

147 therefore the data was further screened to remove movements on these days. The

148 remaining sample size for statistical analysis contained 6,521 locations in the South and

149 5,308 locations in the North.

150

151 *Habitat Data*

152 Habitat maps were generated using ArcMap Ver 9.3.1 (ESRI 2009) with shapefiles that

153 contained ground cover information generated by Svenska Marktäckedata (Hagner *et al.*

154 2005). The ground cover maps were last updated in 2002 and have a resolution of 25m x

155 25m. The map was updated with data of harvested forest stands (clear-fellings) available

156 for the years 2003 to 2005 (from the Swedish forestry board). The ground cover maps were

157 used in the home range and habitat selection analysis.

158

159 *Movement modelling*

160 We used the approach outlined by Papworth et al. (2012) linking net-squared displacement
 161 to identify movement, resting and feeding phases, utilisation distribution to quantify the
 162 area used during the three phases and the resource utilisation function to analyse habitat
 163 selection (Fig 1).

164

165 To identify movement phases (Fig 2), we used the dispersal approach outlined by
 166 Bunnefeld *et al.* (2011) and Börger & Fryxell (2012). Two dispersal models were fitted;
 167 one describing the movement from the resting ground to the feeding ground (the “outward
 168 journey”) and one for the journey from the feeding ground back to a resting ground (the
 169 “return journey”). Each model analysed a 12 hour time period in order to identify the
 170 expected movements at dawn or dusk and the stationary period on either side of a
 171 movement when deer are either feeding or resting. The 12 hour time periods lasted
 172 between midday and midnight to detect the expected peak of activity at dusk and dawn.
 173 The outward and return journeys were modelled using a logistic model, equivalent of a
 174 dispersal strategy used in Bunnefeld *et al.* (2011) and Börger & Fryxell (2012).

175

$$176 \text{ NSD} = \frac{\delta}{1 + \exp\left(\frac{\theta - t}{\phi}\right)} \quad \text{Eqn1}$$

177

178 where δ is the asymptotic height (in km^2), θ is the timing (in minutes) at which the
 179 movement reaches half its asymptotic height, ϕ models the timing (in minutes) elapsed
 180 between reaching $\frac{1}{2}$ and $\sim\frac{3}{4}$ of the asymptote and t is the number of minutes since trip
 181 start.

182

183 The dispersal strategy was also compared to alternative movement models of home range,
184 nomadism and a null model, as described in Börger & Fryxell (2012) and Singh et al.
185 (2012). Model fit was evaluated using the Concordance Criterion (CC), which ranges
186 between -1 and 1, where a CC value <0 indicates lack of fit and higher CC values indicate
187 improved fit (Huang, Mang & Yang 2009; Singh *et al.* 2012). Individual red deer and trip
188 were added as random effects to account for the fact that movement data were nested
189 within individuals and that there were multiple trips by the same individual. We tested
190 whether the asymptote (δ), timing (θ) and duration (ϕ) differed between January, February
191 and March by adding month as a fixed effect. Different combinations of fixed effects were
192 modelled with the random effects to determine the best model structure, indicated by the
193 CC value. Once the best random effects structure had been determined, movement
194 parameters were generated for the North and South study sites using month as a fixed
195 effect to determine whether movements were influenced by the differing hours of sunlight
196 during the study period. The analysis was performed using R software (R Development
197 Core Team 2012, Version 2.15.0). Movement trajectories and NSD were calculated using
198 the package Adehabitat (Calenge 2006). The data was then modelled using nonlinear
199 mixed effect models in the statistical package nlme (Pinheiro *et al.* 2012). The results of
200 the model provided estimates for the distance, timing and duration of movements.

201

202 *Utilisation Distribution (UD)*

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

$$206 J_s = S + (\theta - 2\phi)$$

Eqn2

207 $J_e = S + (\theta + 2\phi)$ Eqn3

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

212

213 Separate UD's were calculated for feeding and resting behaviour using the biased-random
 214 bridge (BRB) method (Benhamou & Cornélis 2010; Benhamou 2011). All 12 individuals
 215 met the minimum number of 200 locations recommended for UD analysis (Millsbaugh *et*
 216 *al.* 2006; Benhamou & Cornélis 2010). The diffusion coefficient was calculated using the
 217 function BRB.D (Benhamou 2011) in the package Adehabitat (Calenge 2006). Once the
 218 UD had been calculated, the area of use at the 50% and 95% isopleths was calculated using
 219 the function kernel.area function in Adehabitat (Calenge 2006). The UD for deer in each
 220 study area was combined and the mean taken to compare between the North and South
 221 study areas. Once the UD had been computed, a further test was performed to understand
 222 how the travelling speed of an individual was correlated to the proportion of open habitats
 223 in an individual's UD. The average speed during the travelling phase (Fig 2) was
 224 calculated and the open habitats included were "Arable land" and "Pastures". The
 225 correlation was estimated using the Pearson's product-moment correlation coefficient in R
 226 (R Development Core Team 2012, Version 2.15.0).

227

228 *Resource Utilisation Function (RUF)*

229 The shapefile containing the UD for each individual was loaded into ArcMap together with
 230 the ground cover map for the region. Any points with a UD >95 were excluded, therefore
 231 only grid squares with a 95% probability of use would be analysed. The dominant habitat

232 for each 25m x 25m grid cell was extracted using Spatial Join in the Geoprocessing tool
233 reference. The package RUF, version 1.5.2 (Handcock 2012), was used to analyse the UD.
234 The log of (100-UD) was used as the response variable to give a normal distribution
235 (Kerston & Marzluff 2010; Papworth *et al.* 2012). The explanatory variable used was the
236 habitat type. The range and smoothness parameters were estimated by the model using a
237 Matern correlation function (Marzluff *et al.* 2004; Millspaugh *et al.* 2006). The mean
238 smoothness for the feeding dataset was 0.64 and 0.90 for the resting dataset. The mean
239 range was 38.31m for the feeding dataset and 27.10m for the resting dataset. The
240 standardised coefficient was calculated as this allows the comparison of the relative
241 influence of resources on animal use whereas the unstandardised coefficient is used to map
242 predicted use of resources (Marzluff *et al.* 2004). The RUF for each deer was combined
243 and the mean calculated for each study area in order to compare RUFs according to
244 landscape structure.
245

246 **Results**

247

248 *Movement Patterns*

249 The best fitting model for the movement patterns of all red deer was the dispersal model
250 (Fig S1), for both outward and return journeys, using a random effects structure that
251 included trip nested within individual and that these varied with the fixed effects of month
252 for the asymptote (δ), timing (θ) and duration (φ).

253

254 Red deer in the South travelled further than deer in the North on both outward and return
255 journeys (Fig 3, Table 1), with a number of trips ($n=27$ of 170) in excess of 2km for the
256 South, compared with just three trips (of 111) exceeding 2km in the North. Red deer in
257 both regions travelled further on the outward journey compared to the return journey,
258 although this difference was greater in the South, with an average difference of 0.48km
259 compared to the North with an average difference of 0.18km. The timing of the outward
260 journey was generally later by 60 minutes in the South and the return journey was on
261 average 40 minutes earlier compared with the North. The duration of outward journeys
262 were fairly similar in both regions (125 minutes) despite deer travelling further in the
263 South. A noticeable difference was that the return journey took 30 minutes longer in the
264 North compared to the South (summary in Fig 3, Table 1). The average speed whilst
265 travelling had a significant positive correlation with the proportion of open habitat within
266 an individual's UD ($r = 0.764$, $n = 12$, $P = 0.004$), with the average speed increasing as the
267 proportion of open habitat increases (Fig 4).

268

269 Red deer exhibited different responses in the two study sites with the timing of their
270 outward and return journeys in relation to sunrise and sunset (Table 2). In January, red deer

271 in both regions left the resting place after sunset and returned before sunrise. However, in
272 February they exhibited differing behaviour with red deer in the North, leaving the resting
273 place before sunset in contrast to the South which left after sunset. Red deer in both
274 regions returned before sunrise in February though. In March, red deer altered their
275 strategies again. Red deer in the North still left the resting place before sunset, but now
276 returned after sunrise. Red deer in the South also left the resting place before sunset but
277 continued to return to the resting place before sunrise.

278

279 *Utilisation Distribution (UD)*

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

284

285 *Resource Utilisation Function (RUF)*

286 Younger forest during resting was the only habitat to be selected for in both study sites,
287 whilst arable land was avoided in both areas during resting (Table S3, Fig 5). The habitats
288 selected for while feeding varied across the two study areas. Red deer in the North strongly
289 selected for clear-felled areas and had lower selection for pastures and coniferous forest
290 $>15\text{m}$. Red deer in the South showed some selection for arable land and pastures, but in
291 contrast to the North, an avoidance of clear-felled areas. While resting, red deer in both
292 study sites selected for clear-felled areas and younger forest, however, the South also
293 selected for broad-leaf forest, coniferous forest 5 - 15m and coniferous forest $>15\text{m}$.

294

295 **Discussion**

296

297 Landscape structure and the relative availability of different habitat components in the
298 landscape influenced the daily movement patterns of red deer between feeding and resting
299 locations and the utilisation of these areas. The NSD movement model revealed that the
300 distance travelled between the feeding and resting locations is greater in the South
301 (fragmented, dominated by agriculture) than in the North (mostly covered by forest);
302 however the duration of the journey was longer in the North, particularly for the return
303 journey from the feeding to the resting areas. The UD identified regional differences in the
304 area utilised for both feeding and resting. All red deer in the South had larger UDs than red
305 deer in the North and in some instances, the area utilised was five times larger in the South
306 compared to the North. In both study sites, habitats selected while resting showed a general
307 trend of preference for coniferous forest, younger forest and clear-felled areas and an
308 avoidance of arable land and pastures. The overall habitat selection patterns of red deer in
309 both of our study regions show a functional response in habitat selection (Mysterud & Ims
310 1998), as reported in previous studies of ungulates (Godvik *et al.* 2009; Massé & Côté
311 2009; Bjørneraas *et al.* 2012). However, we also found differences in habitat selection
312 between the southern and northern areas. Red deer increased selection for coniferous forest
313 as the availability of open habitats increased in the South, whereas in the North there was
314 increased selection for open habitats as the availability of forest increased. This indicates
315 that the landscape structure impacts habitat selection patterns of red deer in Sweden. These
316 patterns of selection are also influenced by the daily activity rhythms of individuals, as
317 feeding patterns took place in open but exposed habitats whereas resting patterns were in
318 forested and sheltered habitats. Therefore, red deer in southern Sweden experience a trade-
319 off between food and cover (Mysterud & Østbye 1999; Godvik *et al.* 2009).

320

321 Red deer in the South show a general trend of selection for most forest types whilst resting,
322 in a landscape dominated by agriculture. Although the forest stands provide cover, they
323 provide little in the way of available forage (Myrsterud & Østbye, 1999), which may result
324 in higher levels of bark stripping as observed in previous studies (Månsson & Jarnemo,
325 2012). Coniferous forests >15m were also selected whilst feeding, alongside open, exposed
326 habitats of arable land and pastures. This segregation of habitat selection clearly indicates a
327 trade-off between using sheltered habitats during the day and foraging habitats at night.

328 Red deer in the North had higher levels of selection for clear-felled forest and younger
329 forest whilst resting. These habitats are a form of human-induced succession, allowing new
330 plants species to colonise the ground and field layer thus increasing the supply of forage
331 and cover for ungulates (Kuiters, Mohren, & Van Wieren 1996; Bergquist, Örlander &
332 Nilsson 1999). Red deer in the North also had higher levels of selection for clear-felled
333 forests during feeding. Therefore, it appears that red deer in the North use clear-felled
334 forests for both food and cover, meaning that they experience less of a trade-off compared
335 with the South.

336

337 The differing patterns of habitat selection and the trade-off between food and cover are
338 supported by the movement patterns of red deer. Red deer in both regions appear to exhibit
339 movement patterns that are influenced by disturbance. In regions with little or no
340 disturbance, red deer are active during the day and night (Clutton-Brock, Guinness &
341 Albon 1982; Kamler, Jedrzejewska, & Jedrzejewski 2007), whereas disturbance causes
342 shifts in activity patterns to night (Georgii 1981; Pepin, Morellet & Goulard 2009), as
343 observed in this study. However, the activity patterns varied in the two regions and the
344 need for cover may explain the differences between the North and the South. In our study,

345 the distance travelled by red deer in the South was greater but completed over a shorter
346 duration. Arable land and pastures may be perceived as open, risky habitats (Mysterud &
347 Østbye, 1999), therefore red deer in the South do not leave the shelter of the forest until
348 after sunset and return to the forest before sunrise, thus using darkness as a form of cover
349 whilst in these open habitats. Movement theory reviewed by Fahrig (2007) indicates that
350 animals moving through risky or low-resource habitats have straighter movement paths,
351 therefore minimising the time spent there, and that spatial aggregation of habitats would
352 favour shorter movement distances. This theory is supported by our results as red deer with
353 a higher proportion of open habitats in their UD had higher travelling speeds. The greater
354 distances travelled by deer in the South also suggests that the habitats that provide food
355 and shelter are segregated in the landscape. In contrast, red deer in the North had shorter
356 movements over a longer duration, suggesting that they are moving through less risky
357 habitats and that the habitats that provide food and shelter are more aggregated in the
358 landscape. Therefore, the trade-off between food and cover may be lower in the North,
359 which is why the timing of movements is not so strictly aligned to the hours of darkness.

360

361 The space use patterns of red deer may also provide insights into the structure of habitats
362 selected by red deer. The average UD was at least twice as large in the South compared to
363 the North. The intra-specific variation in the size of home ranges is still poorly understood
364 (Anderson et al. 2005, Said & Servanty 2005), with explanations that include seasonal
365 variation, availability of resources and shelter, (Tufto, Andersen & Linnell 1996; Anderson
366 et al. 2005; Börger *et al.* 2006). However, theory suggests that as resources become scarce
367 across the landscape, or distributed over a wider area, organisms may need to operate at
368 larger spatial scales in order to meet their demands (O'Neill *et al.* 1988). The larger UDs in
369 the South supports this theory, along with the habitat selection and movement patterns

370 reported above. The habitats that provide food and cover are more segregated in the South,
371 meaning that red deer need to operate at larger spatial scales to meet their demands. In
372 contrast, habitats that provide food and cover are more aggregated in the North, so red deer
373 are able to operate at smaller spatial scales and hence utilise a smaller portion of the
374 landscape. These differing movement patterns show how changes in the landscape
375 structure influence the movement and feeding behaviour of red deer in the two study
376 regions.

377

378 The methodology framework appears to have been appropriate in correctly identifying
379 several behavioural characteristics of red deer reported in previous studies. The results of
380 the UD and RUF confirm that during winter, red deer are feeding (active) at night and
381 resting (inactive) during the day (Georgii 1981; Green & Bear 1990; Godvik et al. 2009).
382 Separating these behaviours is important for habitat selection studies (Myserud & Ims,
383 1998; Godvik et al. 2009), and the combination of methods used in this study has provided
384 an objective and accurate means of differentiating between these movement states and
385 linking them to space use and habitat selection. Through the unified framework applied in
386 this study, one is able to gain a better understanding of how, why, when and where an
387 animal moves, thus advancing the movement ecology paradigm (Nathan et al. 2008). The
388 generality of the approach means that this unified framework can be applied to the
389 increasing number of species able to carry GPS devices.

390

391 Our study has shown how various methods in movement ecology can be combined to
392 further our understanding of the behavioural responses of red deer in landscapes with
393 contrasting habitats and level of fragmentation. The variation influenced by differences in
394 the landscape structure is reflected in the functional responses of red deer and their space

395 use patterns. This knowledge has important management implications, as the trade-off
396 between food and cover may influence the levels of bark stripping (Månsson & Jarnemo
397 2012). Management actions that improve the spatial distribution and availability of
398 resources in the landscape may contribute towards alleviating this human-wildlife conflict,
399 potentially avoiding the need to reduce deer numbers. The results from studies such as
400 these are vital for furthering our ecological understanding of species adaptation to human-
401 induced changes in the landscape, and adapting management strategies to these ecological
402 responses.
403

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580 **Figures**

581

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

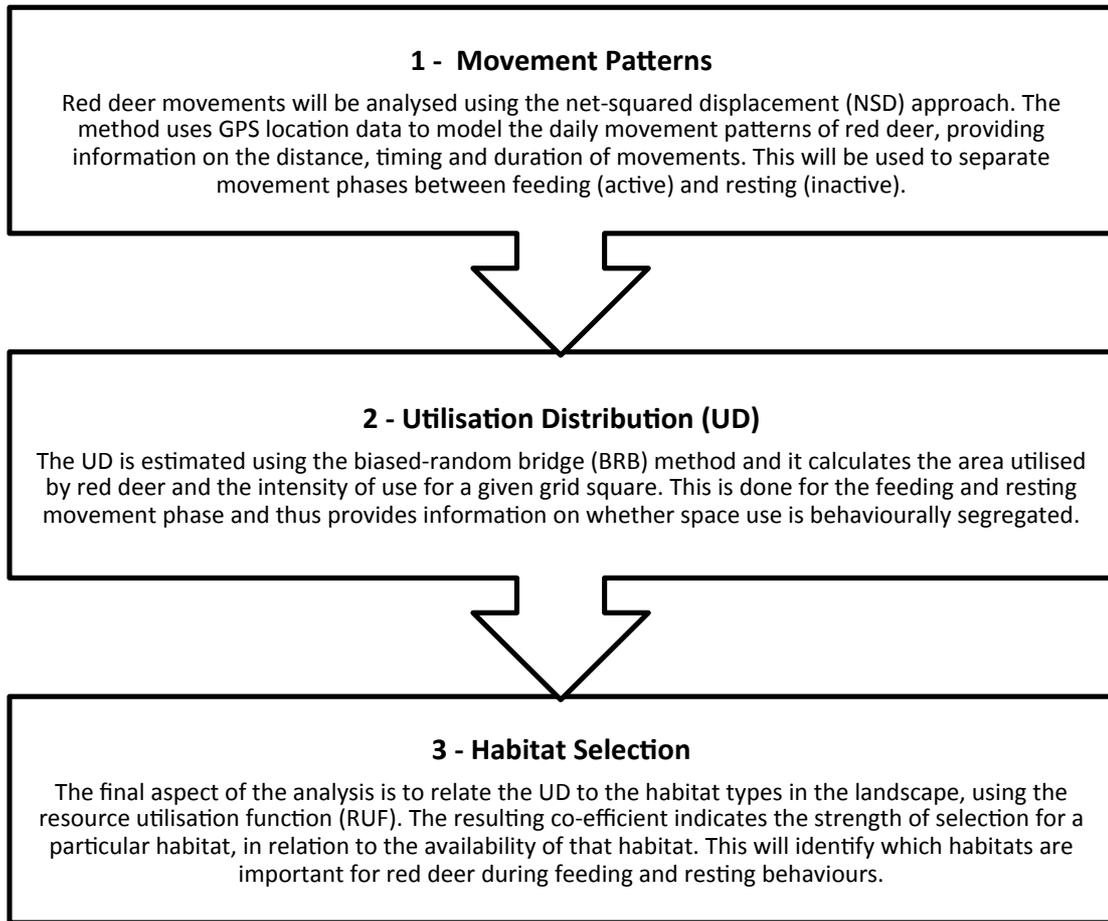
584 **Figure 2** – The theoretical daily movement patterns of a central place forager showing the
585 variation in net displacement over a 24 hour time period (solid black line). Our study
586 divides this movement into two segments, the outward journey (right) and the return
587 journey (left). The results of Eqn1 are used to estimate the feeding (diagonal lines) and
588 resting (shaded grey) times based on when a red deer returns to or leaves the
589 feeding/resting ground.

590 **Figure 3** - Outward and Return journeys for the North and the South. Trips are shown as
591 grey points with connecting lines and the modelled output as a solid black line

592 **Figure 4** – Travelling speed in relation to percentage cover of open land correlation ($R^2 =$
593 0.58). Travelling speed is the average speed in metres per hour during “travelling” phases,
594 i.e. the time period during which red deer are moving to or from the resting/feeding areas.
595 Percentage cover of open land is the proportion of arable land and pastures contained
596 within an individual’s UD. Solid black points are red deer in the North, white points are
597 red deer in the South.

598 **Figure 5** - Standardised resource utilisation function (RUF) coefficients by habitat type,
599 for feeding and resting, in the North and the South study sites. Positive RUF values
600 indicate that use of a resource is greater than expected based on availability and negative
601 RUF values indicate that use of a resource is less than expected based on availability. The
602 error bars indicate the 95% confidence limits.

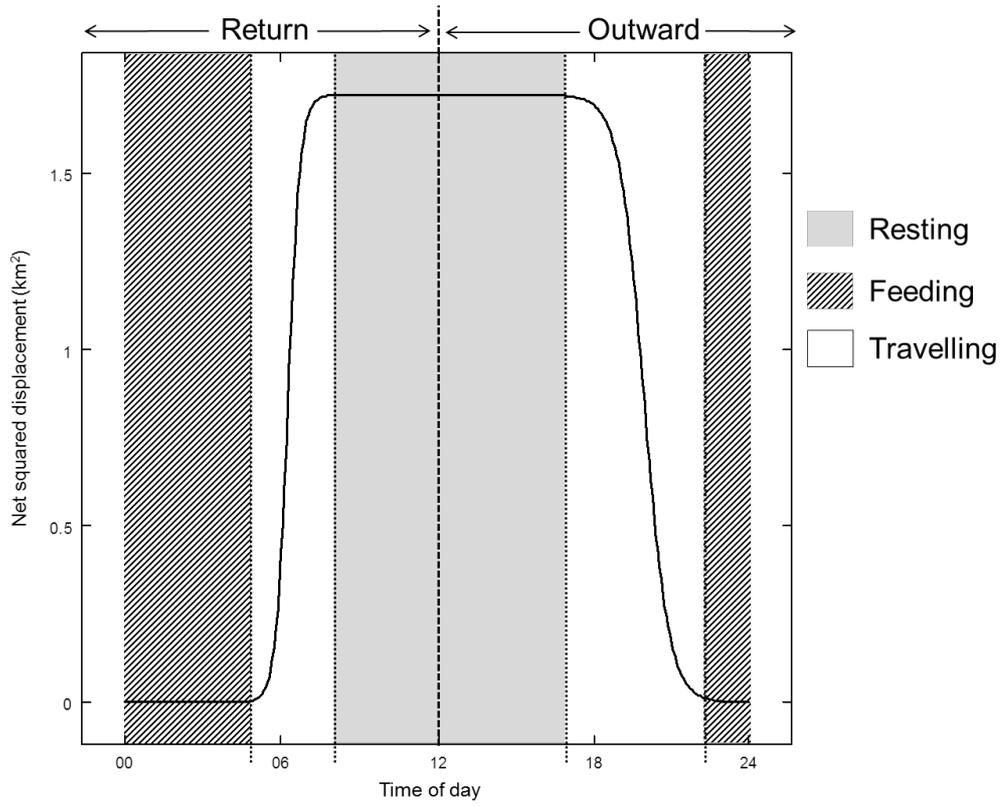
603 **Figure 1**



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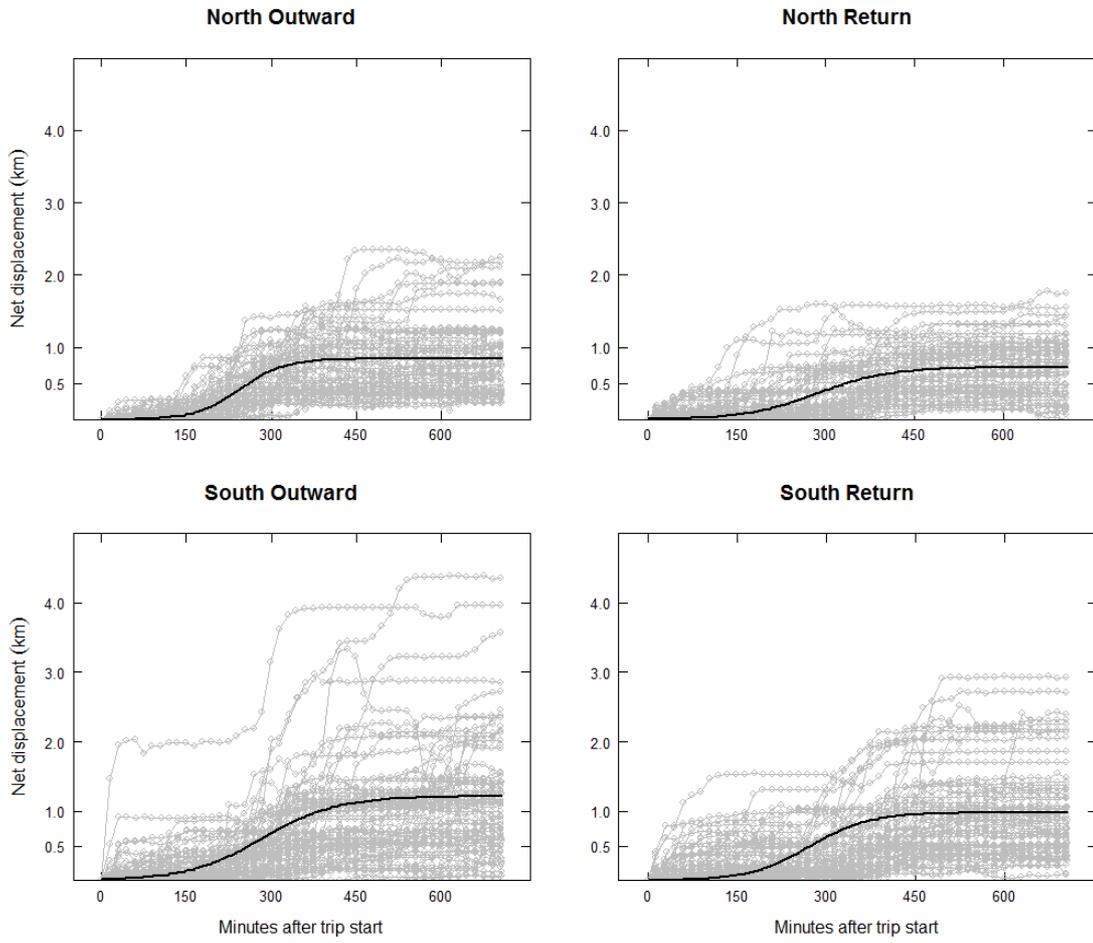
606 **Figure 2**



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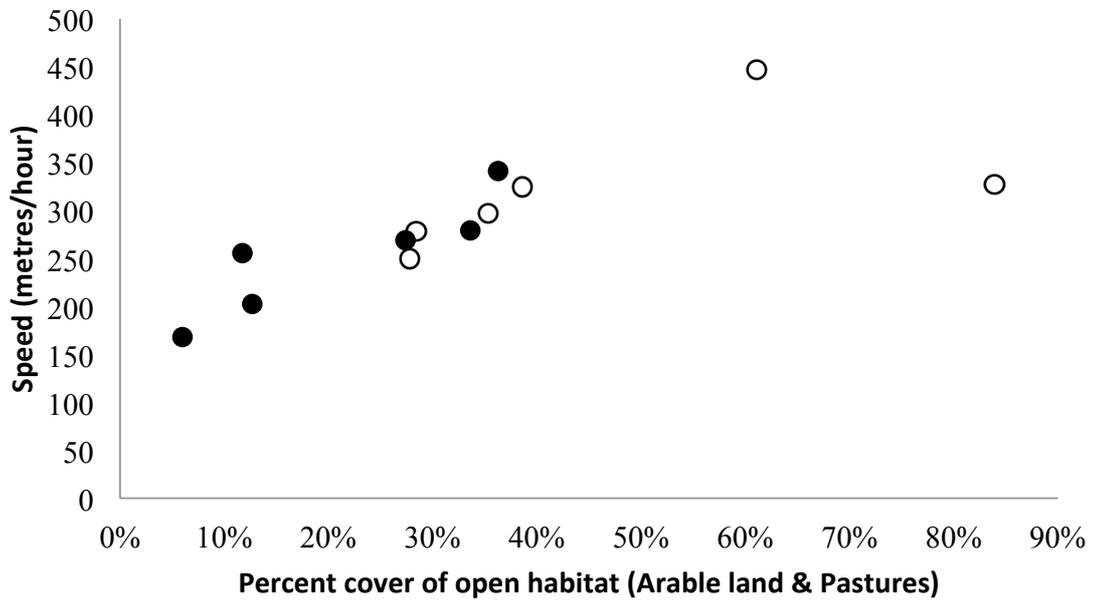
609 **Figure 3**



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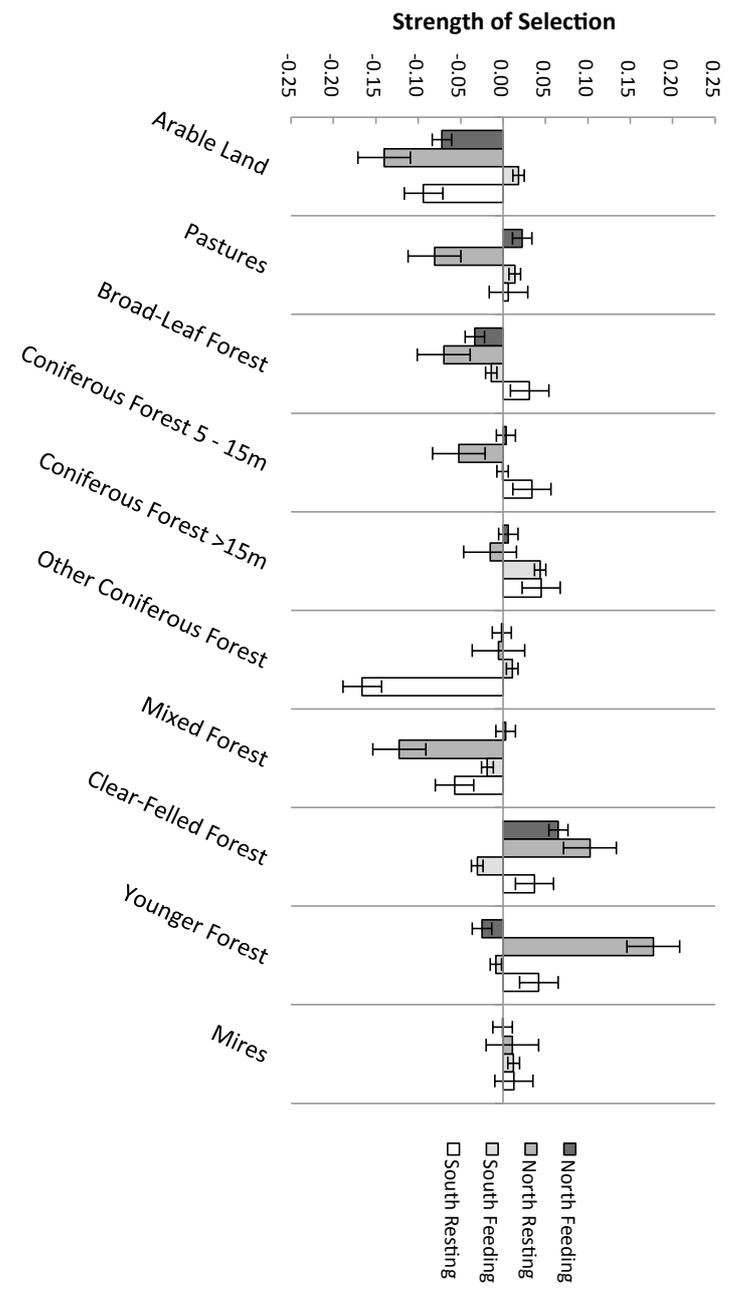
612 **Figure 4**



613

614 **Figure 5**

615



616 **Tables**

617

618 **Table 1** Net Squared Displacement (NSD) model outputs (see Eqn 1) for outward and
 619 return journeys in the North (top) and South (bottom) with 95% confidence intervals (C.I.),
 620 where δ is the asymptotic height (converted to km), θ is the timing (in minutes) at which
 621 the movement reaches half its asymptotic height and ϕ is the timing (in minutes) elapsed
 622 between reaching $\frac{1}{2}$ and $\frac{3}{4}$ 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

623

624

625 **Table 2** Comparison of timing that a red deer leaves the resting area (outward) or returns
 626 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

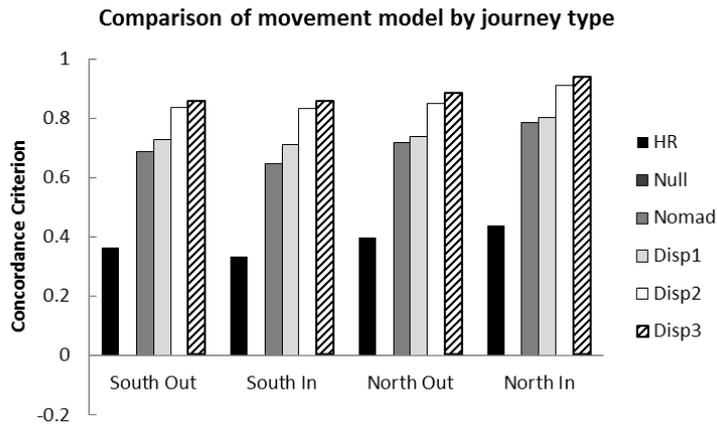
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629 **Supporting Information**

630

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

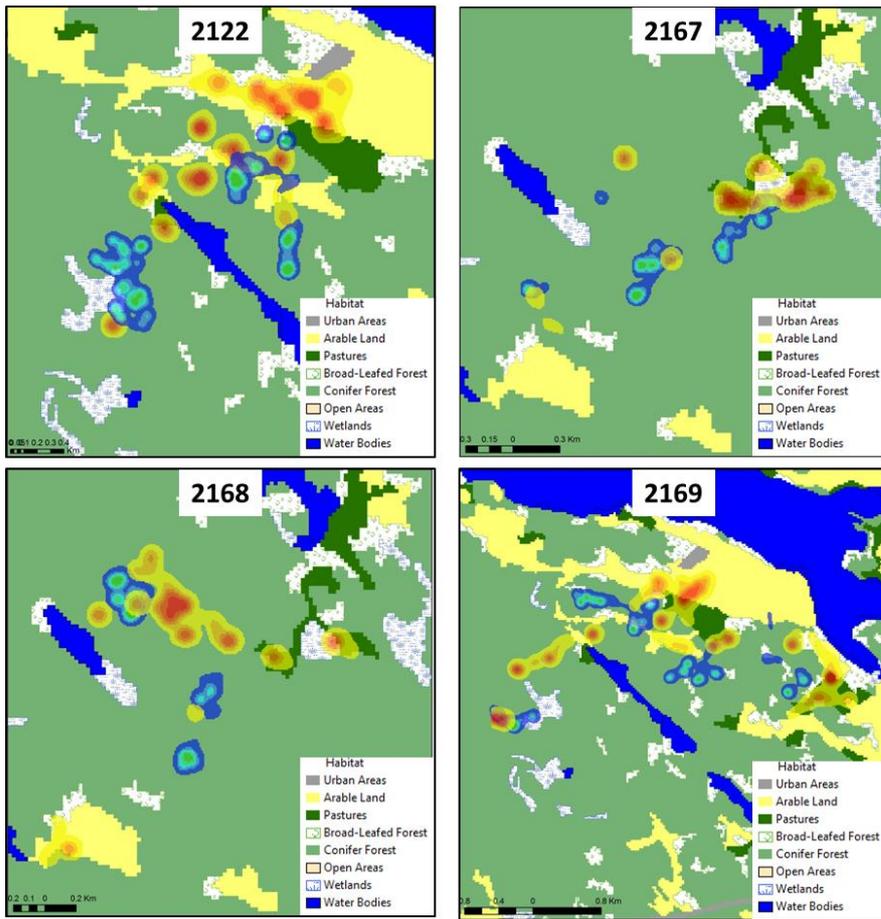


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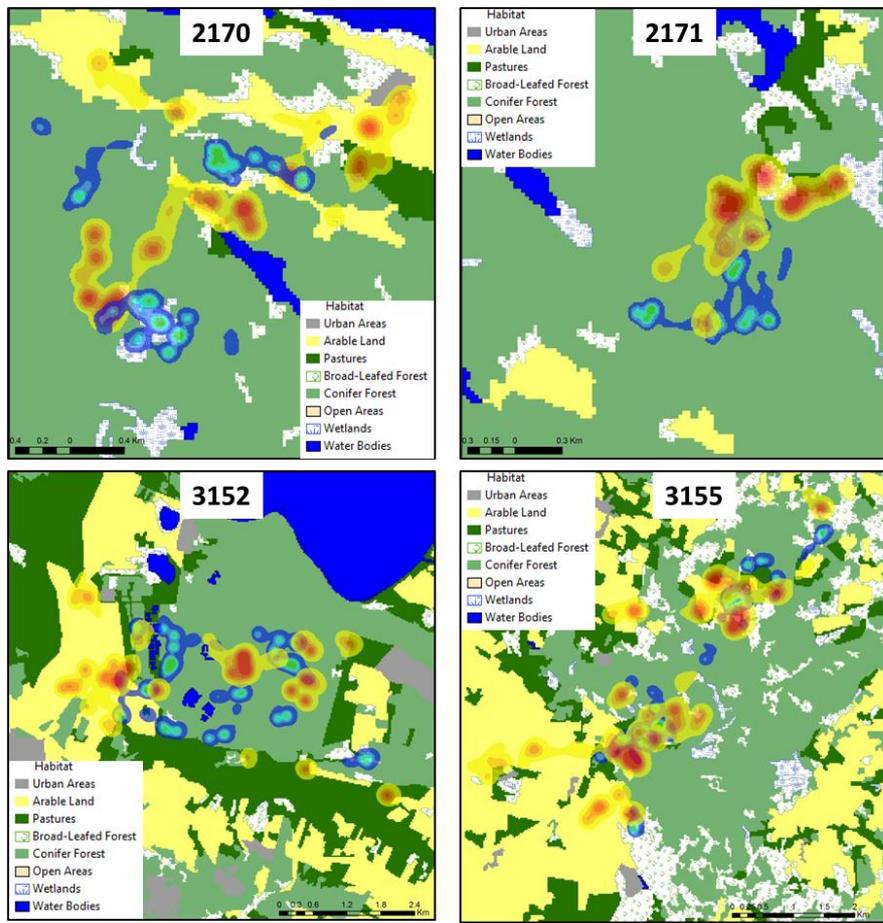
639 **Figure S2** – Utilisation distribution (UD) maps for all red deer in the North (IDs 2122 to
 640 2171) and South (IDs 3152 to 3200). The intensity of use for feeding is indicated by a
 641 graduated scale from yellow (low intensity) to red (high intensity). The intensity of use for
 642 resting is indicated by a graduated scale from blue (low intensity) to green (high intensity).
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648 **Figure S2 (cont.)**

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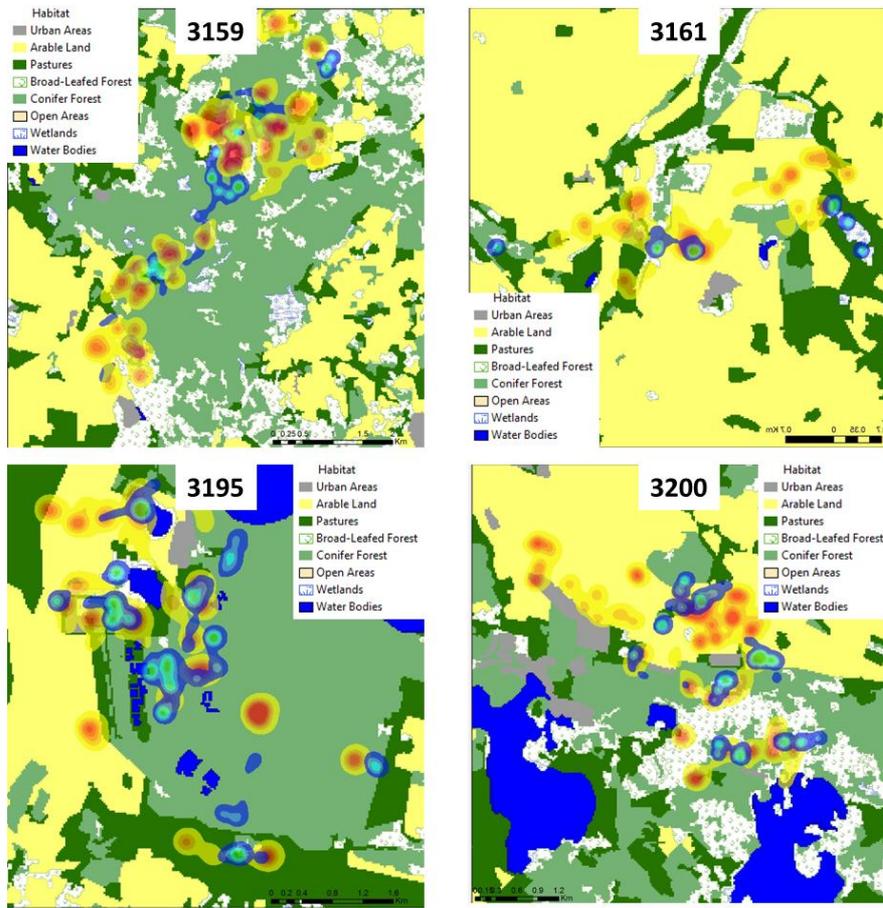


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652 **Figure S2 (cont.)**

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655

656 **Table S1** Feeding and resting times for red deer used for the analysis of the utilisation
 657 distribution (UD)
 658

	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

659

660

661 **Table S2** – Utilisation distribution area (in km²) for the feeding and resting dataset, for
 662 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

663

664 **Table S3** – Resource utilisation function results for Feeding (top) and Resting (middle) for
 665 each individual sorted for the North (2122 to 2171) and the South (3152 to 3200), with the
 666 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		

667

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		

668

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

669 Appendix S1 – GPS Data Screening

670

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

687

688 The second type of error in GPS data is location error. A location error is the difference
689 between an animal's true location and the position recorded by a GPS collar (Bjørneraas *et*
690 *al.* 2010). Location errors may result in the misclassification of habitats used in resource
691 selection functions (Visscher 2006) and may introduce bias into movement data (Hurford
692 2009). There are two measures of accuracy for a GPS location; these are the number of
693 satellites and the satellite geometry. A two-dimensional (2D) fix is when three satellites are

694 recorded simultaneously and a three-dimensional (3D) fix is four or more satellites (Lewis
695 *et al.* 2007). Satellite geometry is measured by the dilution of precision (DOP) and a low
696 DOP value represents higher accuracy due to improved triangulation by the satellites
697 (Langley 1999). The GPS data collected during the study period has a high degree of
698 accuracy as over 95% of records have 3D fixes and over 97% of records have a DOP of
699 less than 10 metres. Some screening methods suggest the removal of 2D fixes (D'Eon *et*
700 *al.* 2002; Lewis *et al.* 2007) or points with a high DOP (D'Eon & Delparte 2005), or a
701 combination of the two (Lewis *et al.* 2007). These screening methods could result in the
702 loss of between 1,200 to 16,000 data points for this study, depending on the method used.
703 Instead, a recently adapted method, which incorporates the movement characteristics of an
704 animal, will be used to screen the data for location errors. The method outlined in
705 Bjørneraas *et al.* (2010) uses two steps to identify potential location errors. The first step
706 identifies locations farther away than a pre-set distance from surrounding points and the
707 second step identifies erroneous spikes in turning angle and speed. Based on knowledge of
708 red deer movement and behaviour in the study areas, the following parameters were used
709 in the screening model:

710

711 $\Delta = 10\text{km}$ 712 $\mu = 5\text{km}$ 713 $\alpha = 1.5 \text{ km/hour}$ 714 $\theta = 0.97$

715

716 where Δ is a large, predefined distance that the animal is unlikely to travel within the
717 maximum sampling interval, μ is a large, predefined distance that the animal is not likely
718 to have travelled, α is a predefined threshold for speed and θ is a predefined threshold for

719 turning angle (Bjørneraas *et al.* 2010). The screening method was done using the open-
720 source statistical software R (R Development Core Team 2012, Version 2.15.0) and it
721 requires the package Adehabitat (Calenge 2006). This method detected a total of 98
722 location errors that were removed from the dataset.

723

724 **References (Appendix S1)**

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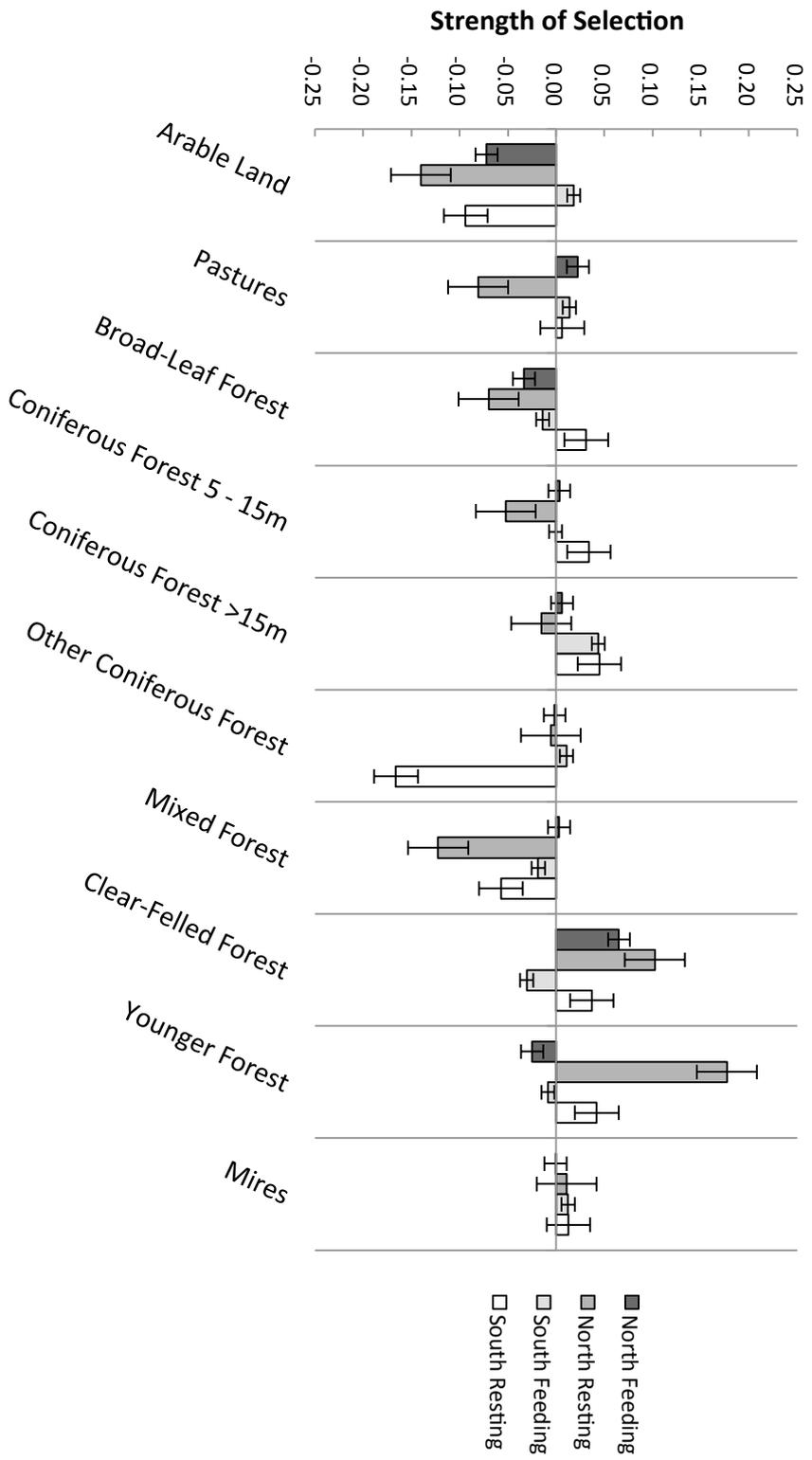
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614 **Figure 5**

615



616 **Tables**

617

618 **Table 1** Net Squared Displacement (NSD) model outputs (see Eqn 1) for outw

619 return journeys in the North (top) and South (bottom) with 95% confidence in

620 where δ is the asymptotic height (converted to km), θ is the timing (in minutes621 the movement reaches half its asymptotic height and ϕ is the timing (in minutes622 between reaching $\frac{1}{2}$ and $\sim\frac{3}{4}$ 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	0.87
	February	1.06	0.93	0.87	0.87
	March	0.93	0.92	0.81	0.81
	Average	1.05	0.91	0.87	0.87
Timing (θ) (minutes)	January	346.4	59.0	413.8	59.0
	February	297.4	65.9	346.7	65.9
	March	307.3	65.1	356.8	65.1
	Average	317.0	63.3	372.4	63.3
Duration (ϕ) (minutes)	January	29.9	22.0	40.8	22.0
	February	33.2	27.0	39.7	27.0
	March	28.9	27.4	47.8	27.4
	Average	30.7	25.5	42.8	25.5
South					
Asymptote (δ) (km)	January	1.51	1.24	1.29	1.24
	February	2.04	1.53	1.23	1.53
	March	1.42	1.55	1.01	1.55
	Average	1.66	1.44	1.18	1.44
Timing (θ) (minutes)	January	366.6	57.6	359.2	57.6
	February	439.8	87.6	367.9	87.6
	March	347.7	91.1	273.9	91.1
	Average	384.7	78.8	333.7	78.8
Duration (ϕ) (minutes)	January	29.5	14.5	29.4	14.5
	February	39.6	21.8	35.1	21.8
	March	32.5	24.1	34.5	24.1
	Average	33.9	20.1	33.0	20.1

623

624

625 **Table 2** Comparison of timing that a red deer leaves the resting area (outward) or returns
 626 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

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628

629 **Supporting Information**

630

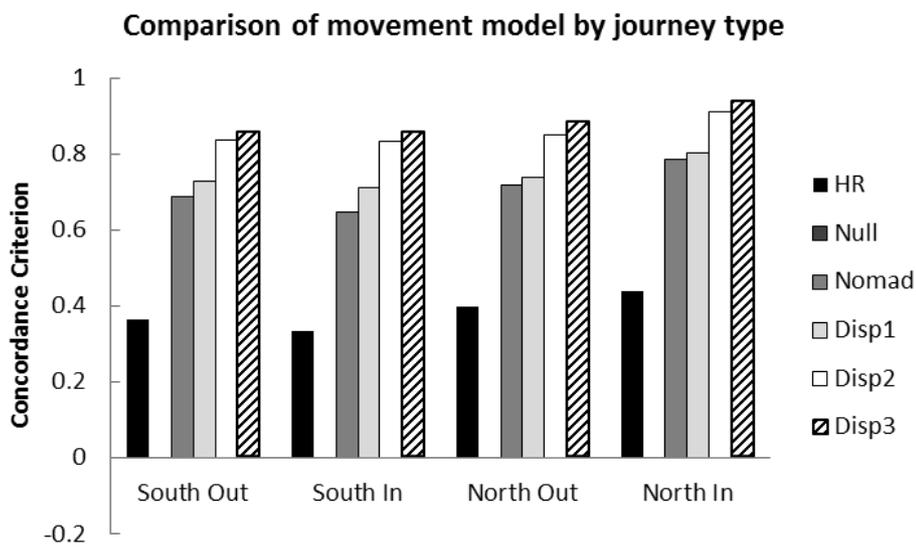
631 **Figure S1** – Concordance Criterion (CC) values for each movement model: HR = Home

632 Range model, Null = Null model, Nomad = Nomadic model, Disp1 = Dispersal model that

633 includes asymptote (δ) as a random effect, Disp2 = Dispersal model that includes

634 asymptote (δ) and timing (θ) as random effects, Disp3 = Dispersal model that includes

635 asymptote (δ), timing (θ) and duration (φ) as random effects.

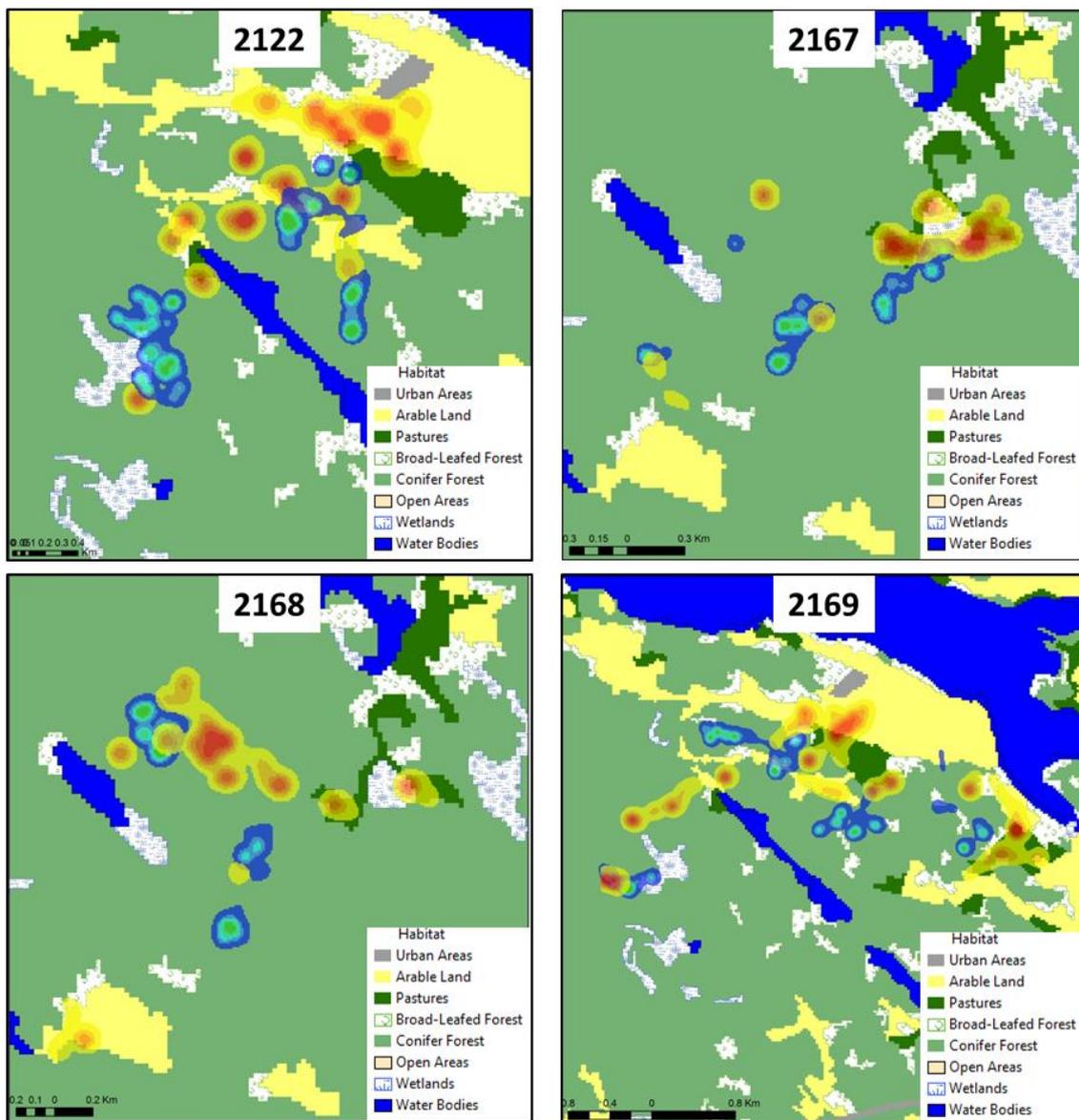


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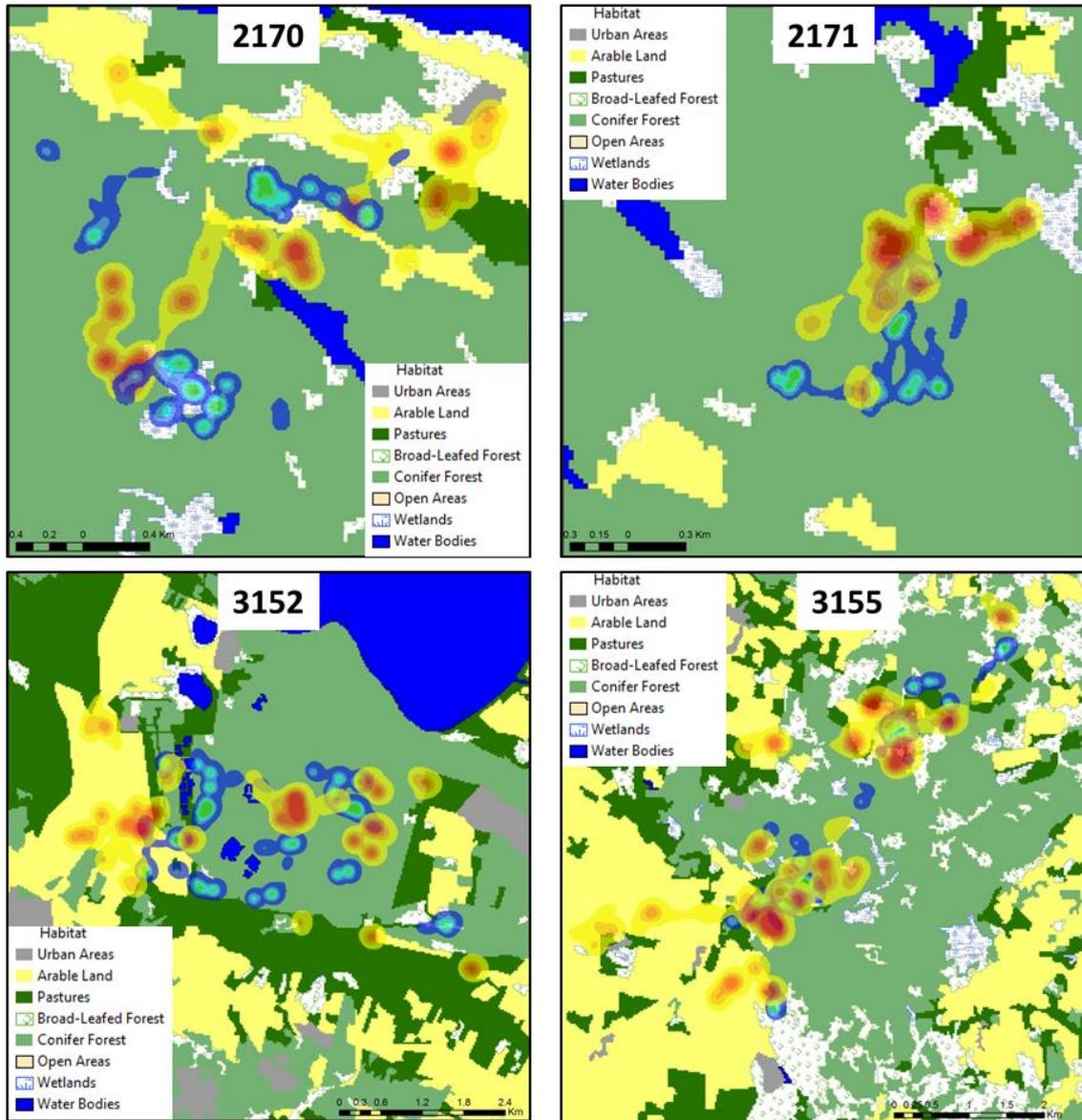
639 **Figure S2** – Utilisation distribution (UD) maps for all red deer in the North (IDs 2122 to
 640 2171) and South (IDs 3152 to 3200). The intensity of use for feeding is indicated by a
 641 graduated scale from yellow (low intensity) to red (high intensity). The intensity of use for
 642 resting is indicated by a graduated scale from blue (low intensity) to green (high intensity).
 643
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 647

648 **Figure S2 (cont.)**

649

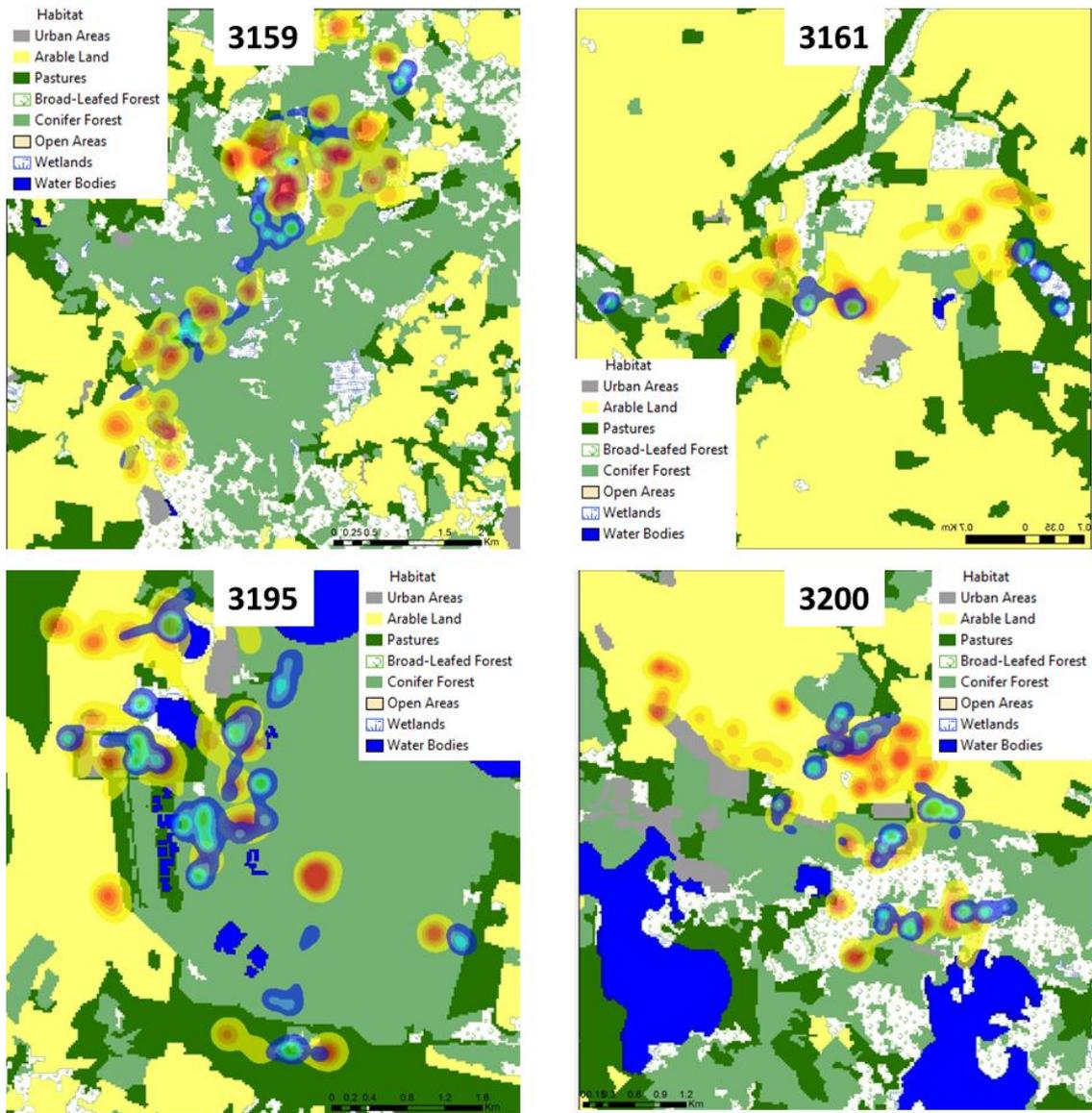


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652 **Figure S2 (cont.)**

653



654

655

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

658

	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

659

660

661 **Table S2** – Utilisation distribution area (in km²) for the feeding and resting dataset, for
 662 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

663

664 **Table S3** – Resource utilisation function results for Feeding (top) and Resting (middle) for
 665 each individual sorted for the North (2122 to 2171) and the South (3152 to 3200), with the
 666 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		

667

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		

668

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

669 Appendix S1 – GPS Data Screening

670

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

687

688 The second type of error in GPS data is location error. A location error is the difference
689 between an animal's true location and the position recorded by a GPS collar (Bjørneraas *et*
690 *al.* 2010). Location errors may result in the misclassification of habitats used in resource
691 selection functions (Visscher 2006) and may introduce bias into movement data (Hurford
692 2009). There are two measures of accuracy for a GPS location; these are the number of
693 satellites and the satellite geometry. A two-dimensional (2D) fix is when three satellites are

694 recorded simultaneously and a three-dimensional (3D) fix is four or more satellites (Lewis
695 *et al.* 2007). Satellite geometry is measured by the dilution of precision (DOP) and a low
696 DOP value represents higher accuracy due to improved triangulation by the satellites
697 (Langley 1999). The GPS data collected during the study period has a high degree of
698 accuracy as over 95% of records have 3D fixes and over 97% of records have a DOP of
699 less than 10 metres. Some screening methods suggest the removal of 2D fixes (D'Eon *et*
700 *al.* 2002; Lewis *et al.* 2007) or points with a high DOP (D'Eon & Delparte 2005), or a
701 combination of the two (Lewis *et al.* 2007). These screening methods could result in the
702 loss of between 1,200 to 16,000 data points for this study, depending on the method used.
703 Instead, a recently adapted method, which incorporates the movement characteristics of an
704 animal, will be used to screen the data for location errors. The method outlined in
705 Bjørneraas *et al.* (2010) uses two steps to identify potential location errors. The first step
706 identifies locations farther away than a pre-set distance from surrounding points and the
707 second step identifies erroneous spikes in turning angle and speed. Based on knowledge of
708 red deer movement and behaviour in the study areas, the following parameters were used
709 in the screening model:

710

711
$$\Delta = 10\text{km}$$

712
$$\mu = 5\text{km}$$

713
$$\alpha = 1.5 \text{ km/hour}$$

714
$$\theta = 0.97$$

715

716 where Δ is a large, predefined distance that the animal is unlikely to travel within the
717 maximum sampling interval, μ is a large, predefined distance that the animal is not likely
718 to have travelled, α is a predefined threshold for speed and θ is a predefined threshold for

719 turning angle (Bjørneraas *et al.* 2010). The screening method was done using the open-
720 source statistical software R (R Development Core Team 2012, Version 2.15.0) and it
721 requires the package Adehabitat (Calenge 2006). This method detected a total of 98
722 location errors that were removed from the dataset.

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724 **References (Appendix S1)**

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