SPECIAL FEATURE: STUCK IN MOTION? RECONNECTING QUESTIONS AND TOOLS IN MOVEMENT ECOLOGY

Movement is the glue connecting home ranges and habitat selection

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Summary

1. Animal space use has been studied by focusing either on geographic (e.g. home ranges, species' distribution) or on environmental (e.g. habitat use and selection) space. However, all patterns of space use emerge from individual movements, which are the primary means by which animals change their environment.

2. Individuals increase their use of a given area by adjusting two key movement components: the duration of their visit and/or the frequency of revisits. Thus, in spatially heterogeneous environments, animals exploit known, high-quality resource areas by increasing their residence time (RT) in and/or decreasing their time to return (TtoR) to these areas. We expected that spatial variation in these two movement properties should lead to observed patterns of space use in both geographic and environmental spaces. We derived a set of nine predictions linking spatial distribution of movement properties to emerging space-use patterns. We predicted that, at a given scale, high variation in RT and TtoR among habitats leads to strong habitat selection and that long RT and short TtoR result in a small home range size.

3. We tested these predictions using moose (*Alces alces*) GPS tracking data. We first modelled the relationship between landscape characteristics and movement properties. Then, we investigated how the spatial distribution of predicted movement properties (i.e. spatial autocorrelation, mean, and variance of RT and TtoR) influences home range size and hierarchical habitat selection.

4. In landscapes with high spatial autocorrelation of RT and TtoR, a high variation in both RT and TtoR occurred in home ranges. As expected, home range location was highly selective in such landscapes (i.e. second-order habitat selection); RT was higher and TtoR lower within the selected home range than outside, and moose home ranges were small. Within home ranges, a higher variation in both RT and TtoR was associated with higher selectivity among habitat types (i.e. third-order habitat selection).

5. Our findings show how patterns of geographic and environmental space use correspond to the two sides of a coin, linked by movement responses of individuals to environmental heterogeneity. By demonstrating the potential to assess the consequences of altering RT or TtoR (e.g. through human disturbance or climatic changes) on home range size and habitat selection, our work sets the basis for new theoretical and methodological advances in movement ecology.

Key-words: *Alces alces*, hierarchical habitat selection, home range, movement ecology, residence time, resource selection, time to return

Introduction

Animal space use is a central topic in ecology that has been addressed from two complementary viewpoints: geographic and environmental space. Typically, studies rooted in geographic space focused on individual home range size and spatial distribution (Moorcroft 2012), whereas studies on environmental space aimed to identify factors determining resource use and selection (Manly *et al.* 2002). The observed patterns of space use in both

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geographic and environmental spaces result from an individual's movement process, which is the glue linking home range and habitat selection. In this paper, we first develop a theoretical framework to link movement properties and space use in both geographic and environmental spaces. Then, we test a set of predictions issued from this framework by using GPS data on movement and space use of moose (*Alces alces*).

An animal's space-use pattern in geographic space emerges from all its relocation events (i.e. movements). Although any movement is defined by a change in the geographic space, the animal's decision to move is a response to changes in the environmental space (Van Moorter *et al.* 2013a) to satisfy its requirements in terms of refuge or resources (Nathan *et al.* 2008). In other words, animals do not move for the sake of changing their geographic location, but rather for changing environmental conditions associated with changes in location. Thus, movement occurs in response to the environmental conditions experienced by the animal. It follows that the relationships between environmental characteristics and space-use patterns are the result of their direct relationships with the animal's movements; that is, the environment affects an animal's movements, and these in turn determine its space use. Previous theoretical models have investigated how movement properties affect home range size (Moorcroft & Lewis 2006; Van Moorter *et al.* 2009), and have linked movements to resource selection (Moorcroft & Barnett 2008).

Generally speaking, movement consists of two main components, allowing an animal to seek, access and exploit resources: departure from the previous location and arrival in a new location. To reduce the frequency of leaving a suitable area, individuals should increase residence time by decreasing the speed and increasing the tortuosity of movements. To increase the frequency of visiting suitable areas, individuals should direct their movements towards these areas. The decisions about departure are based on observed or anticipated local environmental conditions (e.g. resource depletion), whereas decisions about visiting a new location are based on expected environmental conditions through perception or memory. The distinction between these two movement components can be found in most conceptual frameworks on animal movement. Mathematical movement models (Mueller & Fagan 2008; Ovaskainen & Crone 2010) distinguish between random movements away from the present location (diffusion) and those directed towards specific locations (advection). This distinction between departure and arrival is functionally similar to the distinction between kinesis and taxis in invertebrates (Benhamou & Bovet 1992), between tactic and strategic movements (Gautestad & Mysterud 2005) or between patch departure and patch choice in optimal foraging theory (Stephens & Krebs 1986).

Following the diversity of theoretical frameworks, a wide range of empirical approaches have been developed to study these movement components (i.e. departure versus arrival). Departure has often been studied using random walk (Bergman, Schaefer & Luttich 2000; Morales *et al.* 2004) and patch-departure approaches (First Passage Time: Fauchald & Tveraa 2003; Patch Residence Time: Barraquand & Benhamou 2008; Optimal Foraging Theory: Stephens & Krebs 1986), while arrival has been mostly investigated based on the properties at the end point of a movement (e.g. Step Selection Functions: Fortin *et al.* 2005). Benhamou & Riotte-Lambert (2012) integrated both movement components explicitly by decomposing the home range into two complementary metrics (called 'intensity' and 'recursion' in their paper). Based on Barraquand & Benhamou (2008), we define intensity as the residence time (RT) corresponding to the time spent in a given area and recursion as the time to return (TtoR) corresponding to the time it takes to return to this area after the individual has left it. Previous studies suggest that these two main movement components (i.e. RT and TtoR) shape animal space use both in geographic (Moorcroft & Lewis 2006; Van Moorter *et al.* 2009) and in environmental spaces (Bastille-Rousseau, Fortin & Dussault 2010).

In the geographic space, mechanistic home range models have demonstrated the central role of both RT and TtoR (Moorcroft & Lewis 2006; Börger, Dalziel & Fryxell 2008; Van Moorter *et al.* 2009). Van Moorter *et al.* (2009) showed that decreased RT and increased TtoR lead to increased home range size. Similarly, Moorcroft & Lewis (2006) showed that increased diffusion or decreased advection leads to increased home range size. Furthermore, several empirical studies have documented smaller home ranges in more favourable environments, where RT is expected to be higher and/or TtoR to be lower (e.g. roe deer *Capreolus capreolus*: Tufto, Andersen & Linnell 1996; moose *Alces alces*: Bjørneraas *et al.* 2012; langur *Trachypithecus leucocephalus*: Li & Rogers 2005).

In the environmental space, Bastille-Rousseau, Fortin & Dussault (2010) showed that the selective use of some environmental features results from increased RT in preferred habitats or from increased revisitation of preferred habitats. Benhamou & Riotte-Lambert (2012) showed that areas with longer stays and areas with higher revisitation rate are not necessarily the same. For instance, transit areas or water holes are often visited but for only brief periods of time. Likewise, Anderson, Forester & Turner (2008) did not find any correspondence between RT in a given habitat and individual preference for that specific habitat. We may therefore expect that increased use of these habitats resulted from a decreased TtoR.

In this paper, we first develop a theoretical framework to explain the mechanistic relationship between movement properties and animal use of geographic and environmental spaces. As resource selection is typically viewed as a hierarchical process where an individual first

selects its home range from the available landscape (second-order habitat selection) and therein selects habitat patches (third-order habitat selection; Johnson 1980), we explore the link between movement, home range size and hierarchical habitat selection. Secondly, from this theoretical framework, we derive a set of nine predictions (Fig. 1), which we test in two steps using a large sample of GPS tracking data of moose in Norway. In the first step, we model the relationship between movements and environmental characteristics. In general, we expect RT and TtoR to be similarly affected by favourable environmental conditions because individuals are expected to stay longer and return earlier to favourable habitats than to unfavourable ones. In the second step, we investigate how the spatial distribution of predicted movement characteristics affects home range size and habitat selection using the nine predictions issued from our theoretical framework.

Theoretical framework

We predict that, independently from the scale of observation, a high variation in RT and TtoR among habitats should be associated with strong habitat selection and that short RT and long TtoR should be associated with large home range size. We elaborated nine predictions (P1–P9, Fig. 1). The predictions P1–P6 explain how movement links the different space-use components, and the predictions P7–P9 link space-use patterns in geographic and environmental spaces.

GEOGRAPHIC SPACE

Shorter RT (P1a) and longer TtoR (P1b) should lead to increased home range size. This prediction is based on previous works by Mitchell & Powell (2004), Moorcroft & Lewis (2006), and Van Moorter *et al.* (2009). Mitchell & Powell (2004) further predicted that increased spatial autocorrelation in RT and TtoR should result in decreased home range size. Indeed, increased spatial autocorrelation in the landscape should lead to increasing selection in the positioning of the home range (P4a and P4b; see below for further details). This, in turn, should result in an increased concentration of favourable resources within the home range, which should be associated with increased RT and decreased TtoR (P2a and P2b). The overall effect of these processes should lead to decreased home range size (back to P1a and P1b).

ENVIRONMENTAL SPACE

Habitat selection is the process by which individuals choose a specific habitat type among a set of available habitat types, whereas habitat preference occurs from a selection under the condition of equal availability (Johnson 1980; Lele *et al.* 2013; Van Moorter *et al.* 2013b). Studies of hierarchical habitat selection have commonly focused on two spatial scales: selection of the home range in the landscape and selection of resources within the home range (called second- and third-order habitat selections, respectively, *sensu* Johnson 1980). It can be shown that the difference
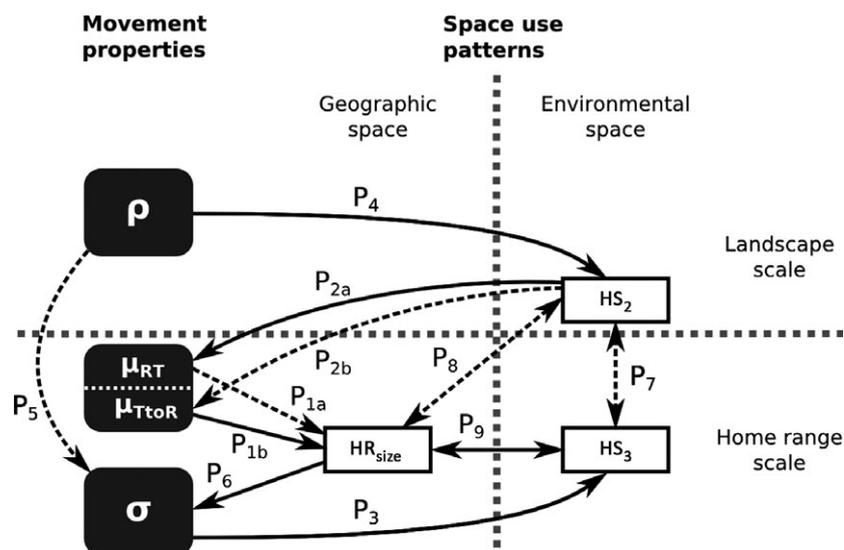

Fig. 1. Predicted relationships among movement characteristics (filled boxes) and individual space-use patterns (squared boxes). Space use is characterized by home range size (HR_{size}) in the geographic space, and by selection of the home range in the landscape (i.e. HS_2: second-order habitat selection) and of patches within the home range (i.e. HS_3: third-order habitat selection) in the environmental space. Residence time (RT) and time to return (TtoR) are characterized by their within-home range mean and variance (μ and σ), and by their landscape autocorrelation (ρ). Predicted positive and negative causal relationships are indicated by solid and dashed arrows, respectively. To reduce the number of arrows, we did not distinguish between RT and TtoR, when the direction of their predicted effects was the same (i.e. σ and ρ). Predicted indirect correlations among space-use patterns are indicated by double arrows. The numbers on the arrows correspond to the predictions in the mean text and the Table 4. See text for further explanations.

between the mean characteristic of the available and used habitats ($\partial\bar{x}$, a measure of habitat selection) equals the variance of the characteristic (σ_x^2) times the animal's preference (*pref*[*]) for it (Appendix S1, Supporting information):

$$\partial\bar{x} = pref* \times \sigma_x^2. \qquad\qquad \text{eqn 1}$$

Thus, habitat selection is dependent upon the animal's preference and the variation in the possibility of choice. Therefore, the strength of habitat selection within the home range should depend upon the variation in RT and TtoR in relation to available habitats within the home range (P3a and P3b).

We can mathematically demonstrate that variation in movement properties at the landscape scale can be decomposed into within- and between-home range variations (Appendix S2). This is similar to the decomposition into α- (within-habitat) and β- (between-habitat) biodiversities (Whittaker 1960). In reference to this similarity, we call the within- and between-home range variances α- and β-variances, respectively.

$$\sigma_\gamma^2 = \sigma_\alpha^2 + \sigma_\beta^2 \qquad\qquad \text{eqn 2}$$

When variation in movement properties among home ranges is large (high σ_β^2), the variance of movement properties within the home range is relatively small (low σ_α^2), when controlling for the overall variance (i.e. σ_γ^2 is constant). Moreover, for a given home range size, the variation in the movement properties among home ranges (σ_β^2) increases with increasing spatial autocorrelation (Appendix S3). Therefore, the strength of the selection of home range location in the landscape should increase with the autocorrelation of the landscape (P4a and P4b). Similarly, for a given home range size, the variation in movement properties within the home range should decrease (σ_α^2) when spatial autocorrelation increases (P5a and P5b), while controlling for the overall variance. Finally, for a given spatial autocorrelation, the variation in movement properties within home ranges should increase with home range size (P6a and P6b; see Appendix S3).

RELATING GEOGRAPHIC AND ENVIRONMENTAL SPACE USE

The aforementioned predictions P1–P6 (Fig. 1) explain how movement links the different space-use components. Three additional predictions complete the framework linking space-use patterns in geographic and environmental spaces. In the environmental space, within- and among-home range selections should be negatively correlated (P7) in response to the opposing effects of autocorrelation on the variation in movement properties within and among home ranges (as stated in P5a and P5b). Home range size should be negatively correlated with the strength of selection among home ranges (P8) because of the effect of home range selection on mean RT and TtoR (as stated in P2a and P2b) and their subsequent effect on home range size (P1). Finally, the positive relationship between home range size and within-home range variation in movement properties (as stated in P6a and P6b) and their subsequent positive effect on third-order habitat selection (P3) should lead to a positive correlation between the within-home range selection and home range size (P9).

We tested all these predictions on female moose that were monitored using GPS and for which high-quality data were available on movement properties, home range size and habitat selection, both within and among individual home ranges.

Materials and methods

STUDY AREA

The study area covers a large portion of central Norway (Fig. 2a) and ranges from coastal areas with boreonemoral characteristics to alpine zones over continuous altitudinal gradients. Coniferous and, to a lesser extent, deciduous forests dominate hilly areas, while cultivated land is only widespread at lower altitudes (Moen 1999). The habitat types used most frequently by monitored female moose included the following (in order of decreasing frequency, see Table A1 in Appendix S4): dense coniferous forest (type 0: 27%), open coniferous forest (type 1: 17%), deciduous forest (type 3: 13%), bilberry – birch forest (type 5: 8%), tall herb – deciduous forest (type 4: 6%) and bogs (type 8: 5%). These habitat types represented more than 75% of land cover types used by moose (for details regarding vegetation types see Johansen, Aarrestad & Øien 2009). We limited our study to the summer period and focused on spatial variation only.

DATA

We monitored 171 individuals from a partially migratory population during 2006–2008: 7 individuals were fitted with Tellus GPS collars (Followit AB/Televilt, Lindesberg, Sweden) and 164 with GPS PLUS/GPS PRO Light collars (VECTRONIC Aerospace GmbH, Berlin, Germany). Capture, handling and anaesthetizing of female moose were all approved by the Norwegian Directorate for Nature Management and the Research Animal Committee in Norway (Approvals 2005/44882-3, 07/1059-07/6838-3 and 07/68902). We programmed GPS collars to obtain one location every second hour; outliers were detected following Bjørneraas *et al.* (2010) and removed from the data set. We only retained resident moose during summer (July–August) with at least 700 locations (<6% missing fixes). As we investigate home range use, the animals have to be resident within a stable home range during the summer period. Moose residency was determined based on two criteria: monthly range overlap and net displacement (ND). First, the monthly ranges from July and August should be highly overlapping. We required a Volume of Intersection (Kernohan, Gitzen & Millspaugh 2001) of at least 50% between the kernel utilization distributions of both months. Secondly, we performed a linear regression of ND against time and required resident moose to have a relatively flat slope (i.e. slope <1·25 m h⁻¹; meaning that a moose was allowed to drift not more than about 2 km within this 2-month period). These two criteria ensured a stable space use during summer (as confirmed by visual

Fig. 2. Study area in central Norway displaying female moose locations (panel a), the relationship between residence time, RT (represented by relative departure risk), and time to return, TtoR (represented by relative return risk; panel b), and the spatial prediction of RT (panel c) and of TtoR (panel d). Note that the values predicted for both the RT and TtoR are associated with the risk of departure and return, respectively. The scales are thus inverted with respect to RT and TtoR, respectively. The results shown in panels b–d are from the analysis with 250 m radius and 12-h time cut-off. Panel b displays in black the most common categories and their trend line, the numbers correspond to the vegetation types in Table A1 (Appendix S4) with W, M and A depicting, respectively, vegetation types 10, 16 and 22.
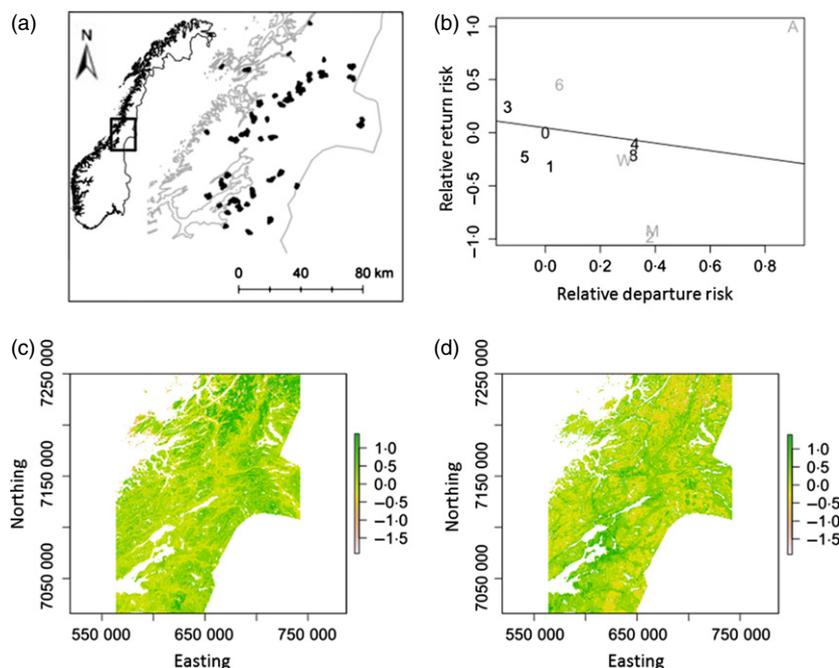
inspection). A total of 48 individuals fulfilled all these criteria. We used a 30-m resolution land cover map developed by the Northern Research Institute, based on the classification of Landsat TM/ETM+ data (Johansen, Aarrestad & Øien 2009). The map was produced in close temporal proximity to the moose tracking data.

ANALYSIS

Our analyses consisted of two parts: first, we determined the relationship between the environment and movement properties (i.e. RT and TtoR). Then, we investigated the relationship between the spatial distribution of predicted movement properties and observed patterns of moose space use.

Residence time is the uninterrupted time an animal remains within a certain radius centred on each location, the time being considered interrupted, when the animal leaves this circle longer than a specified cut-off time (Barraquand & Benhamou 2008). Two parameters are required to determine RT, namely the circle's radius and the cut-off time. TtoR is the uninterrupted time an animal spends before its first return to the circle centred on each location. Returns within a time shorter than the cut-off time are not classified as returns; instead, such a 'return' is considered part of the uninterrupted residency. We used different radii and cut-off times (100 m with 12 h, 250 m with 12 h and 250 m with 24 h) to assess the sensitivity of our results to these spatial and temporal thresholds.

To analyse the effects of habitat characteristics on movement properties, we used time-to-event analysis (specifically a Cox proportional hazard model; see Freitas *et al.* 2008), with land cover type and individual identity as explanatory variables. We included individual identities as fixed effects to estimate individual differences in movement properties, which were used in the analyses described below. Due to the large amount of data ($n = 38\ 707$), we found statistically significant deviations from the constant and proportional hazards assumptions. However, visual inspection of the results revealed the effect size of these violations to be minimal. The land cover types were calculated as the proportion of each type within the radius estimated for RT and TtoR.

We then investigated how the spatial distribution of predicted movement properties affects the observed patterns of space use in both geographic and environmental spaces. From the proportion of each habitat type within a radius matching the analysis, we predicted for each pixel the risk of departure or return (for RT and TtoR, respectively) given an average animal (for computational convenience, we used a spatial resolution of 100 m). We predicted the relative risk of an event (i.e. departure or return) using the linear predictor for each radius and cut-off time combination. As higher predicted values from the RT and TtoR analyses correspond to shorter RT and TtoR, respectively, we multiplied these values by −1 to facilitate the interpretation.

To test predictions P1–P6 for each moose, we calculated the spatial distribution of the movement properties from the predicted maps. We calculated the autocorrelation of RT and TtoR in a moose's landscape, defined as the circular area within a 10 000 m radius around the barycentre of the summer locations (which corresponds roughly to the mean observed dispersal distance of moose in the study area, Rolandsen *et al.* 2010). The movement properties within the home range were assessed by mean and standard deviation of RT and TtoR for each individual moose. The autocorrelation was calculated as the range of the fitted spherical variogram function. The range of a variogram is the distance at which the variogram value becomes constant with respect to lag distance (i.e. there is no longer autocorrelation in the values). Thus, a variable displaying a variogram with a large range has autocorrelation up to long distances, whereas the opposite is true for a variable with a small range in its variogram.

The three space-use patterns for which we investigated the effect of movement properties were as follows: home range size, selection of the home range in the landscape (second-order habitat selection; Johnson 1980) and habitat selection within the home range (third-order selection). Home range size was measured during summer as the area in the 95%, 75% and 50% contours of kernel UD ($h = 200$). As these estimates were highly correlated ($r > 0.9$), we only present results for the 95% contours. We measured habitat

selection using resource selection functions (RSF; Manly *et al.* 2002) by comparing used with available locations. For the second-order selection, we sampled *n* available locations randomly from a circular area (10 000 m radius) centred on the median coordinates, whereas *n* used home range locations were sampled randomly from the 95% kernel UD contour (*n* equalled the number of locations for each animal). For the third-order selection, we sampled *n* available locations randomly from the 95% kernel UD contour, whereas used locations were the actual *n* positions of each animal. For each animal, we separately calculated a RSF using land cover types as a predictor in a logistic regression (Manly *et al.* 2002). As a measure of an individual's strength of habitat selection, we evaluated the predictive power of this individual-based RSF (Boyce *et al.* 2002). We used a leave-one-out or jack-knife cross-validation with the area under the curve (AUC) of the receiver operating curve (ROC) to evaluate the performance of the RSF in predicting used versus available locations. The AUC measures the strength of the difference between the used and the available locations based on their environmental characteristics, which is equivalent to the strength of habitat selection.

We tested our predictions using linear regression between movement and space-use patterns. All regressions included standardized variables to facilitate comparison of effect sizes among variables and analyses. We tested our predictions by fitting the following models:

P1: $HR_{size} = id + \mu_{HR} + \varepsilon$.
P2: $(\mu_{HR} - \mu_{LS}) = HS_2 + \varepsilon$.
P3: $HS_3 = \sigma_{HR} + \varepsilon$.
P4: $HS_2 = \rho_{LS} + \varepsilon$.
P5–P6: $\sigma_{HR} = \rho_{LS} + HR_{size} + \sigma_{LS} + \varepsilon$.

where: μ_{HR} and μ_{LS} are the home range and landscape mean of RT or TtoR; ρ_{LS} is the autocorrelation of RT or TtoR in the landscape; σ_{HR} and σ_{LS} are the home range and landscape standard deviation of RT or TtoR; HR_{size} is the home range size; id is the individual effect on RT or TtoR; and HS_3 and HS_2 are third- and second-order habitat selections. Predictions 7–9 were tested using Pearson correlation tests:

P7: corr (HS_2, HS_3).
P8: corr (HS_2, HR_{size}).
P9: corr (HR_{size}, HS_3).

All analyses were performed in R (R Core Team 2013), using the packages 'SP' (Bivand, Pebesma & Gomez-Rubio 2008), 'RASTER' (Hijmans & van Etten 2012), 'ADEHABITATHR' (Calenge 2006) and 'SURVIVAL' (Therneau & Grambsch 2000).

Results

RESIDENCE TIME ANALYSIS

Not surprisingly, the time spent near a location increased with the radius and the cut-off time: 90% of the departures occurred in <16 h for a 100 m radius with a cut-off time of 12 h, 38 h for a 250 m radius (and a 12 h cut-off time) and 56 h with a 24-h cut-off time (and 250 m radius). The large differences in RT among individuals and habitats remained relatively stable across thresholds. Individual differences between thresholds were highly correlated ($P < 0.01$): from 0.85 (between RT at 100 m/12 h

and RT at 250 m/24 h) to 0.96 (between RT at 100 m/12 h and RT at 250 m/12 h). Individual RTs ranged between ±60% of the average. Habitat differences between thresholds also correlated strongly ($P < 0.05$): from 0.51 (between RT at 100 m/12 h and RT at 250 m/24 h) to 0.87 (between RT at 100 m/12 h and RT at 250 m/12 h). The 250 m radius and 12-h cut-off showed the highest correlation with both other thresholds, and we therefore present the parameter estimates for this model.

Moose stayed about 30% longer in deciduous forest (type 3) compared to dense coniferous forest (type 0; Table 1). By contrast, an increase in the proportion of other classes (within the 250 m radius) led to a decreased RT (*c.* 30% for types 1, 5 and 4). RT in bogs was 57% lower than in dense coniferous forest.

TIME TO RETURN ANALYSIS

Return rates were markedly lower than departure rates (i.e. average TtoR was larger than RT), and often, animals did not return to a previously visited site during the study period. The time to a return in the vicinity of a location decreased with radius and increased with cut-off time: 50% of returns occurred in less than 502 h (about 21 days) for a 100 m radius with cut-off time of 12 h, 194 h (about 8 days) for a 250 m radius (and 12 h cut-off time) and 262 h (about 11 days) with a 24-h cut-off time (and 250 m radius). As with the analysis of RT, differences among individuals remained relatively stable across thresholds ($P < 0.01$) and correlated from 0.81 (between TtoR at 100 m/12 h and TtoR at 250 m/24 h) to 0.96 (between TtoR at 250 m/12 h and TtoR at 250 m/24 h). Individual differences in TtoR, on all thresholds, ranged between ±60% of the average. However, habitat differences in TtoR were only highly correlated between the two analyses at the 250-m threshold (i.e. 12 h vs. 24 h cut-off time, $r = 0.93$, $P < 0.001$). The correlations between spatial thresholds were not statistically significant ($r = 0.31$, $P > 0.05$, between 100 m/12 h and 250 m/12 h, and $r = 0.20$, $P > 0.05$, between 100 m/12 h and 250 m/24 h). The 250 m radius and 12-h cut-off time showed the highest correlation with both other thresholds, and we therefore present the parameter estimates for this model.

Compared to dense coniferous forest (type 0; Table 2), animals returned about 60% sooner to areas with deciduous forest (type 3). By contrast, a decreased proportion of dense coniferous forest generated by an increase in any other vegetation type (except deciduous forest) led to increased time to return in an area (of around 25% for types 1, 5 and 8). For these most common habitat types, RT and TtoR were strongly negatively correlated ($r = -0.85$, Fig. 2b), as expected.

LANDSCAPE PATTERNS IN RT AND TtoR

The RT and TtoR models were used to predict RT and TtoR over the landscape based upon the habitat type

Table 1. The effects of the proportion of each of the main vegetation types on the time-to-event analysis of the residence time for each radius and time cut-off combination (i.e. radius/cut-off 100 m/12 h, 250 m/12 h and 250 m/24 h), compared with dense coniferous forest (code = 0). The vegetation codes correspond to open coniferous forest (1), low herb – deciduous forest (3), tall herb – deciduous forest (4), bilberry – birch forest (5) and bogs (8). For all habitat types, see Table A2 in Appendix S4

Code	100 m/12 h				250 m/12 h				250 m/24 h			
	Coef	exp (coef)	SE (coef)	*P*-value	Coef	exp (coef)	SE (coef)	*P*-value	Coef	exp (coef)	SE (coef)	*P*-value
1	0·02	1·02	0·04	0·67	0·27	1·32	0·07	<0·001	0·57	1·77	0·07	<0·001
3	−0·14	0·87	0·03	<0·001	−0·30	0·74	0·06	<0·001	−0·10	0·90	0·06	0·07
4	0·33	1·39	0·06	<0·001	0·29	1·33	0·10	<0·01	−0·06	0·94	0·10	0·53
5	−0·08	0·93	0·05	0·16	0·19	1·21	0·10	0·05	0·72	2·05	0·10	<0·001
8	0·32	1·38	0·06	<0·001	0·45	1·57	0·09	<0·001	−0·02	0·98	0·09	0·81

Table 2. The effects of the proportion of each vegetation type on the time-to-event analysis of the time to return for each radius and time cut-off combination (i.e. radius/cut-off 100 m/12 h, 250 m/12 h and 250 m/24 h), compared with dense coniferous forest (code = 0). The vegetation codes correspond to open coniferous forest (1), low herb – deciduous forest (3), tall herb – deciduous forest (4), bilberry – birch forest (5) and bogs (8). For all habitat types, see Table A3 in Appendix S4

Code	100 m/12 h				250 m/12 h				250 m/24 h			
	Coef	exp (coef)	SE (coef)	*P*-value	Coef	exp (coef)	SE (coef)	*P*-value	Coef	exp (coef)	SE (coef)	*P*-value
1	−0·32	0·73	0·05	<0·001	−0·26	0·77	0·08	<0·001	−0·13	0·88	0·08	0·10
3	0·24	1·27	0·04	<0·001	0·47	1·60	0·06	<0·001	0·56	1·75	0·06	<0·001
4	−0·11	0·90	0·08	0·16	0·03	1·03	0·11	0·81	−0·08	0·93	0·11	0·50
5	−0·23	0·80	0·07	<0·001	−0·31	0·73	0·10	<0·01	−0·14	0·87	0·11	0·20
8	−0·21	0·81	0·08	<0·01	−0·24	0·78	0·10	<0·05	−0·43	0·65	0·10	<0·001

(Fig. 2c–d). The spatial distributions of the predicted RT and TtoR were assessed using their mean, standard deviation and autocorrelation. The threshold-specific correlations between mean and standard deviation of RT and TtoR in the home range were statistically significant (Table 3). Additionally, correlations between the autocorrelation of RT and of TtoR in the landscape at different thresholds were statistically significant (Table 3; the autocorrelations of RT and TtoR were positively skewed and were log-transformed).

At all thresholds, strong negative correlations were observed between mean RT and mean TtoR (all $P < 0.001$; $r = -0.50$, -0.79 and -0.75 for 100 m/12 h, 250 m/12 h and 250 m/24 h, respectively). Positive correlations were found at most thresholds between the variation in RT and TtoR (all $P < 0.001$; $r = 0.91$ and 0.48 for 100 m/12 h and 250 m/12 h, respectively; however, at 250 m/24 h, $r = -0.09$ and $P = 0.55$), and between the autocorrelation of the RT and TtoR ($P < 0.001$; $r = 0.40$ and 0.60 for 100 m/12 h and 250 m/24 h, respectively; however, at threshold 250 m/12 h, $r = 0.20$ and $P = 0.17$).

We expected an increased autocorrelation of RT and TtoR in the landscape to affect negatively the variation in both movement characteristics in the home range (P5a and P5b). We found a negative effect of the landscape autocorrelation on the within-home range variance of RT at 250-m threshold, after controlling for landscape variation (Table 4: P5a). However, there was no such evidence for TtoR (Table 4: P5b).

Table 3. Pearson's correlation coefficients (*r*) and *P*-values for the average (μ), standard deviation (σ) within the animal's home range (HR) and autocorrelation (ρ) of its landscape (LS) for both residence time (RT) and time to return (TtoR) between the different thresholds of analysis (i.e. radius/time cut-off: 100 m/12 h, 250 m/12 h and 250 m/24 h)

	100 m/12 h vs. 250 m/12 h		100 m/12 h vs. 250 m/24 h		250 m/12 h vs. 250 m/24 h	
	r	*P*-value	*r*	*P*-value	*r*	*P*-value
μRT$_{HR}$	0·88	<0·001	0·42	<0·01	0·73	<0·001
σRT$_{HR}$	0·59	<0·001	0·81	<0·001	0·33	<0·05
ρRT$_{LS}$	0·56	<0·001	0·30	<0·05	0·56	<0·001
μTtoR$_{HR}$	0·96	<0·001	0·80	<0·001	0·90	<0·001
σTtoR$_{HR}$	0·81	<0·001	0·27	0·07	0·57	<0·001
ρTtoR$_{LS}$	0·84	<0·001	0·77	<0·001	0·84	<0·001

USE OF THE GEOGRAPHIC SPACE

As the distribution of home range size at 95% was positively skewed, we square-root-transformed this variable (mean $\pm$ SD = 2.9 ± 0.7 km). Additionally, we did not include both RT and TtoR simultaneously into a given model because of the high correlation between mean RT and TtoR at all thresholds. We found the expected negative effects from the mean RT on home range size at all thresholds (Table 4: P1a), and the expected positive effect from the mean TtoR on home range size was statistically significant only at the 250-m threshold (Table 4: P1b).

Individual variation in RT (Table 4: P1) and TtoR (Table 4: P1) had statistically significant effects on home range size at all thresholds.

We did not find any statistically significant effect of home range size on the variation in RT within the home range (Table 4: P6a). However, the within-home range variation in TtoR at the 250-m/12-h threshold increased with the home range size and tended to do so at both other thresholds (Table 4: P6b), after controlling for the landscape variation in TtoR. We did not find evidence for the expected positive correlation between the size and selection within the home range (P9; $r = -0.15$, $P = 0.30$).

USE OF ENVIRONMENTAL SPACE

AUC ranged between 0·5 and 1. As the distribution of AUC of the third-order habitat selection was positively skewed, we log-transformed this variable (log base 10; mean $\pm$ SD $= -0.21 \pm 0.03$). The AUC of the second-order selection was symmetrically distributed (mean $\pm$ SD $= 0.68 \pm 0.05$). We did not find any evidence for the expected negative correlation between second- and third-order selections (P7; $r = 0.12$, $P = 0.40$). As in the previous analysis, we did not include RT and TtoR variables simultaneously in a given model because of their high correlation.

The expected positive effects from the variation in RT on the third-order selection were present at the 12-h thresholds only (Table 4: P3a). However, the expected positive relationship between the variation in TtoR and the third-order selection was present at all thresholds (Table 4: P3b). We found the expected positive effects of the autocorrelation in RT on the second-order selection at 250-m threshold (Table 4: P4a). Conversely, we did not find statistically significant evidence for the expected positive relationship between the range of the autocorrelation in TtoR and the second-order selection (Table 4: P4b).

Increased second-order selection led to a higher mean RT within the home range (Table 4: P2a), and to a lower mean TtoR within the home range (Table 4: P2b), when controlling for the landscape RT and TtoR. Additionally, we also found support for the predicted negative correlation between second-order selection and home range size (P8; $r = -0.36$, $P < 0.05$).

Discussion

Our findings demonstrate that both home range use and habitat selection emerge from movement properties and are thereby the two sides of a same coin. The theoretical framework we propose to assess the link between the distribution of movement properties and their resulting space-use patterns in the geographic space (i.e. home range size) and the environmental space (i.e. habitat selection among and within the home range) was largely supported by high-resolution empirical movement data for female moose in Norway (Table 4).

Table 4. Parameter estimates for the test of predictions presented in Fig. 1 at different spatio-temporal thresholds. In each, Equation β denotes the parameter shown in that row, HR: home range, LS: landscape, RT: residence time, TtoR: time to return, HS: habitat selection [second- (HS_2) and third (HS_3)-order], id: individual effects on RT and TtoR, μ: mean of RT and TtoR, σ: standard deviation of RT and TtoR, ρ: autocorrelation of RT and TtoR, and ε: error term. See the main text for further explanation of the predictions. Parameter estimates highlighted in bold are statistically significant at a 5% level

Pred.	Equation	100 m/12 h			250 m/12 h			250 m/24 h		
		Coef	SE (coef)	P-value	Coef	SE (coef)	P-value	Coef	SE (coef)	P-value
P1	$HR_{size} = \beta * idRT_{HR} + idTtoR_{HR} + \mu RT_{HR} + \mu TtoR_{HR} + \varepsilon$	**-0.34**	**0.07**	**<0.001**	**-0.58**	**0.07**	**<0.001**	**-0.63**	**0.09**	**<0.001**
P1	$HR_{size} = idRT_{HR} + \beta * idTtoR_{HR} + \mu RT_{HR} + \mu TtoR_{HR} + \varepsilon$	**0.69**	**0.07**	**<0.001**	**0.67**	**0.06**	**<0.001**	**0.56**	**0.07**	**<0.001**
P1a	$HR_{size} = idRT_{HR} + idTtoR_{HR} + \beta * \mu RT_{HR} + \varepsilon$	**-0.26**	**0.07**	**<0.001**	**-0.38**	**0.06**	**<0.001**	**-0.22**	**0.09**	**<0.05**
P1b	$HR_{size} = idRT_{HR} + idTtoR_{HR} + \beta * \mu TtoR_{HR} + \varepsilon$	0.14	0.08	0.08	**0.28**	**0.08**	**<0.001**	**0.28**	**0.07**	**<0.001**
P2a	$(\mu RT_{HR} - \mu RT_{LS}) = \beta * HS_2 + \varepsilon$	**0.33**	**0.14**	**<0.05**	**0.43**	**0.13**	**<0.01**	**0.40**	**0.14**	**<0.01**
P2b	$(\mu TtoR_{HR} - \mu TtoR_{LS}) = \beta * HS_2 + \varepsilon$	**-0.39**	**0.14**	**<0.01**	**-0.38**	**0.14**	**<0.01**	**-0.33**	**0.14**	**<0.05**
P3a	$HS_3 = \beta * \sigma RT_{HR} + \varepsilon$	**0.31**	**0.14**	**<0.05**	**0.58**	**0.12**	**<0.001**	0.14	0.15	0.35
P3b	$HS_3 = \beta * \sigma TtoR_{HR} + \varepsilon$	**0.38**	**0.14**	**<0.01**	**0.43**	**0.13**	**<0.01**	**0.58**	**0.12**	**<0.001**
P4a	$HS_2 = \beta * \rho RT_{LS} + \varepsilon$	-0.02	0.15	0.91	**0.46**	**0.13**	**<0.001**	0.27	0.14	0.06
P4b	$HS_2 = \beta * \rho TtoR_{LS} + \varepsilon$	0.23	0.14	0.11	-0.01	0.15	0.96	0.13	0.15	0.37
P5a	$\sigma RT_{HR} = \beta * \rho RT_{LS} + HR_{size} + \sigma RT_{LS} + \varepsilon$	-0.14	0.13	0.28	-0.21	0.12	0.08	**-0.25**	**0.12**	**<0.05**
P5b	$\sigma TtoR_{HR} = \beta * \rho TtoR_{LS} + HR_{size} + \sigma TtoR_{LS} + \varepsilon$	-0.16	0.12	0.18	-0.03	0.13	0.84	0.19	0.12	0.11
P6a	$\sigma RT_{HR} = \rho RT_{LS} + \beta * HR_{size} + \sigma RT_{LS} + \varepsilon$	0.20	0.11	0.09	0.15	0.11	0.18	0.18	0.12	0.13
P6b	$\sigma TtoR_{HR} = \rho TtoR_{LS} + \beta * HR_{size} + \sigma TtoR_{LS} + \varepsilon$	0.19	0.12	0.11	**0.30**	**0.13**	**<0.05**	0.20	0.11	0.07

[Correction added after online publication 24 September 2015: positive and negative signs were reversed in the first six rows of Table 4].

Our results were generally robust to the spatio-temporal thresholds used in the analysis because movement properties were highly correlated among thresholds. Moose stayed longer and returned more frequently to areas with preferred land cover types. We found support for most of the predicted relationships between moose space use and movement properties (Table 4). A shorter mean RT and longer mean TtoR were associated with a larger home range (P1a-b). Increased variance in RT and TtoR was associated with strong habitat selection within the home range (P3a-b), and increased autocorrelation of RT was associated with strong selection of home ranges in the landscape (P4a). However, we did not find support for the expected effect of autocorrelation of TtoR on home range selection (P4b).

We characterized moose movement properties using only two metrics: RT and TtoR. While the former reliably measures the departure from an area in response to the immediate surroundings, TtoR only assesses the arrival rate into previously visited areas. For animals able to assess habitat characteristics at a distance (e.g. through conspecific attraction, Hahn & Silverman 2006), TtoR would miss such directed responses that increase the arrival probability in preferred areas not previously visited. As all individuals we monitored were sedentary adults, we can expect them to have acquired substantial experience with their environment prior to the tracking period. Therefore, RT and TtoR are likely reliable metrics for measuring moose movement properties. For the most common land cover types, we found a negative relationship between RT and TtoR. In areas with denser coniferous forests, that is the most common land cover type, moose stayed longer and returned more frequently than in most other habitat types (e.g. bogs) – except for (dense) deciduous forests in which moose prefer to stay longer (about 30% longer) and return more frequently (about 60% earlier).

Female moose appear to use both RT and TtoR to increase their total time spent in preferred habitat types. In contrast, Anderson, Forester & Turner (2008) found that elk did not increase RT in selected habitats, which they interpreted as an anti-predator tactic resulting in decreased predictability of the individual. In our study area, predation risk was very low (Rolandsen *et al.* 2010). Also, vegetation dynamics could break the negative correlation between RT and TtoR. For instance, when a highly preferred resource takes a long time to renew, high RT and high TtoR should be expected, or when resources are unpredictable, return is no longer an efficient tactic (Mueller, Fagan & Grimm 2011) and animals are expected to increase only their RT.

Previous theoretical studies (Moorcroft & Lewis 2006; Van Moorter *et al.* 2009) have demonstrated that home ranges emerge from movement properties and decreased RT and increased TtoR lead to increased home range sizes. Our empirical study on moose provides evidence that these theoretical predictions do, in fact, hold in free-ranging populations (P1a-b). Mitchell & Powell (2004) further predicted a decrease in home range size when the autocorrelation of

the landscape allows the animals to locate selectively their home range in areas of higher than average quality. Our results support these predictions. We found that individuals that were more selective in the location of their home range had longer average RT (P2a) and shorter average TtoR (P2b), resulting in a negative relationship between second-order habitat selection and home range size (P8).

The possibility for choice only exists when some variation occurs in the choice set. We demonstrated mathematically that habitat selection within home ranges is affected by variation in the habitat-related movement properties. Further, the selective location of home ranges in the landscape is affected by variation among potential home ranges, which is in turn determined by landscape autocorrelation. Indeed, moose were more selective within their home range when the variation in their movement parameters increased (P3a-b) and were more selective in the location of their home range when spatial autocorrelation was higher (P4a).

Rettie & Messier (2000) suggested that the hierarchy of habitat selection depends on the importance of habitat variables limiting individual performance, that is more limiting variables ought to be selected at a higher scale. Our results demonstrate that this hypothesis is incomplete. In fact, Eqn 1 shows that both the preference for a habitat variable and its variation shape the expected pattern of habitat selection. The preference for an environmental variable should be related to its effects on individual fitness. Studies on hierarchical habitat selection that focus solely on the fitness limitation provided by a habitat variable may mistakenly ignore the importance of the variation in the choice set. It is exactly this variation that is crucial for the animal's ability to express selection, as we have demonstrated both theoretically and empirically (Basille *et al.* 2013). Variation is strongly dependent upon spatial scale as measured by its spatial autocorrelation.

A negative relationship should occur between both scales of habitat selection because high spatial autocorrelation leads to a reduced variation in resources within the home range. Contrary to our theoretical model, we did not find any negative relationship between habitat selection within and among home ranges (P7). Several factors can contribute to the absence of this relationship in our data. First, it should be noted that it is the variation within and between home ranges that should be negatively correlated (Eqn 2), not habitat selection *per se*. Indeed, Eqn 1 shows that in addition to variation, preference also affects selection. Further, if preference is scale dependent, the expected relationship could be weakened. We found that variation in movement properties affects habitat selection, but it did not explain all the observed variation in habitat selection (i.e. $\sigma_\varepsilon > 0$ of P3 and P4). Moreover, the relationship between autocorrelation and the variation in movement properties within the home range was weak. The expected relationship only held for RT (and only at large spatial thresholds; P5a): RT became less variable within the home range as the autocorrelation increased in the landscape.

However, we did not find a similar effect on the TtoR (P5b). The difficulty of empirically demonstrating the predicted effects of autocorrelation may be due, in part, to the violation of our assumption of stationarity in real landscapes. Indeed, in real landscapes autocorrelation is a function not only of the distance between locations, but also of the geographical position of these locations in the landscape (i.e. non-stationarity; Miller 2012). The effects of non-stationary autocorrelation for the proposed theory should be investigated in future theoretical studies.

Our study shows how movement characteristics affect space use of individuals. We did not explore the full range of factors influencing animal movements, but we rather focused on habitat relationships. Animal movements are obviously affected by a wide range of factors such as sensory, memory and navigational capacity (Nathan *et al.* 2008), and interactions with conspecifics. We can expect other factors affecting animal movements to alter observed space-use patterns as well. Future research should investigate further the role of these movement mechanisms in this context. Our study provides a formal framework to unify empirical studies on patterns of geographic and environmental space using individual movements as a common mechanism. We demonstrate the central role of variation in movement properties for the study of animal habitat selection. By demonstrating the potential to assess the consequences of altering RT or TtoR (e.g. through human disturbance or climatic changes) on home range size and habitat selection, our work sets the basis for new theoretical and methodological advances in movement ecology.

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Data accessibility

Data available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.58j2m (Van Moorter *et al.* 2015).

References

Anderson, D.P., Forester, J.D. & Turner, M.G. (2008) When to slow down: elk residency rates on a heterogeneous landscape. *Journal of Mammalogy*, **89**, 105–114.

Barraquand, F. & Benhamou, S. (2008) Animal movements in heterogeneous landscapes: identifying profitable places and homogeneous movement bouts. *Ecology*, **89**, 3336–3348.

Basille, M., Van Moorter, B., Herfindal, I., Martin, J., Linnell, J.D.C., Odden, J. *et al.* (2013) Selecting habitat to survive: the impact of road density on survival in a large carnivore. *PLoS One*, **8**, e65493.

Bastille-Rousseau, G., Fortin, D. & Dussault, C. (2010) Inference from habitat-selection analysis depends on foraging strategies. *Journal of Animal Ecology*, **79**, 1157–1163.

Benhamou, S. & Bovet, P. (1992) Distinguishing between elementary orientation mechanisms by means of path analysis. *Animal Behaviour*, **43**, 371–377.

Benhamou, S. & Riotte-Lambert, L. (2012) Beyond the utilization distribution: identifying home range areas that are intensively exploited or repeatedly visited. *Ecological Modelling*, **227**, 112–116.

Bergman, C.M., Schaefer, J.A. & Luttich, S.N. (2000) Caribou movement as a correlated random walk. *Oecologia*, **123**, 364–374.

Bivand, R.S., Pebesma, E.J. & Gomez-Rubio, V. (2008) *Applied Spatial Data Analysis with R*. Springer, New York.

Bjørneraas, K., Van Moorter, B., Rolandsen, C.M. & Herfindal, I. (2010) Screening global positioning system location data for errors using animal movement characteristics. *Journal of Wildlife Management*, **74**, 1361–1366.

Bjørneraas, K., Herfindal, I., Solberg, E.J., Sæther, B.-E., Moorter, B. & Rolandsen, C.M. (2012) Habitat quality influences population distribution, individual space use and functional responses in habitat selection by a large herbivore. *Oecologia*, **168**, 231–243.

Börger, L., Dalziel, B.D. & Fryxell, J.M. (2008) Are there general mechanisms of animal home range behaviour? A review and prospects for future research. *Ecology Letters*, **11**, 637–650.

Boyce, M.S., Vernier, P.R., Nielsen, S.E. & Schmiegelow, F.K.A. (2002) Evaluating resource selection functions. *Ecological Modelling*, **157**, 281–300.

Calenge, C. (2006) The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling*, **197**, 516–519.

Core Team, R. (2013) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Fauchald, P. & Tveraa, T. (2003) Using first-passage time in the analysis of area-restricted search and habitat selection. *Ecology*, **84**, 282–288.

Fortin, D., Beyer, H.L., Boyce, M.S., Smith, D.W., Duchesne, T. & Mao, J.S. (2005) Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology*, **86**, 1320–1330.

Freitas, C., Kovacs, K.M., Lydersen, C. & Ims, R.A. (2008) A novel method for quantifying habitat selection and predicting habitat use. *Journal of Applied Ecology*, **45**, 1213–1220.

Gautestad, A.O. & Mysterud, I. (2005) Intrinsic scaling complexity in animal dispersion and abundance. *The American Naturalist*, **165**, 44–55.

Hahn, B.A. & Silverman, E.D. (2006) Social cues facilitate habitat selection: American redstarts establish breeding territories in response to song. *Biology Letters*, **2**, 337–340.

Hijmans, R.J. & van Etten, J. (2012) raster: raster: Geographic data analysis and modeling. R package version 2.0-41. http://CRAN.R-project.org/package=raster.

Johansen, B., Aarrestad, P.A. & Øien, D.I. (2009) http://www.norut.no/tromso/content/download/4551004/9246892/version/2/file/Norut_rapport_3_2009.pdf

Johnson, D.H. (1980) The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, **61**, 65–71.

Kernohan, B.J., Gitzen, R.A. & Millspaugh, J.J. (2001) Analysis of animal space use and movements. *Radio Tracking Animal Populations* (eds J.J. Millspaugh & J.M. Marzluff), pp. 125–166. Academic Press, San Diego, CA.

Lele, S.R., Merrill, E.H., Keim, J. & Boyce, M.S. (2013) Selection, use, choice and occupancy: clarifying concepts in resource selection studies. *Journal of Animal Ecology*, **82**, 1183–1191.

Li, Z. & Rogers, M.E. (2005) Habitat quality and range use of white-headed langurs in Fusui, China. *Folia Primatologica*, **76**, 185–195.

Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L. & Erickson, W.P. (2002) *Resource Selection by Animals: Statistical Design and Analysis for Field Studies*. Kluwer Academic Publisher, the Netherlands.

Miller, J.A. (2012) Species distribution models: spatial autocorrelation and non-stationarity. *Progress in Physical Geography*, **36**, 681–692.

Mitchell, M.S. & Powell, R.A. (2004) A mechanistic home range model for optimal use of spatially distributed resources. *Ecological Modelling*, **177**, 209–232.

Moen, A. (1999) *National Atlas of Norway: Vegetation*. Norwegian Mapping Authority, Hønefoss, Norway.

Moorcroft, P.R. (2012) Mechanistic approaches to understanding and predicting mammalian space use: recent advances, future directions. *Journal of Mammalogy*, **93**, 903–916.

Moorcroft, P. & Barnett, A. (2008) Mechanistic home range models and resource selection analysis: a reconciliation and unification. *Ecology*, **89**, 1112–1119.

Moorcroft, P. & Lewis, M.A. (2006). *Mechanistic Home Range Analysis*. Princeton University Press, Princeton, New Jersey, USA.

Morales, J.M., Haydon, D.T., Frair, J., Holsinger, K.E. & Fryxell, J.M. (2004) Extracting more out of relocation data: building movement models as mixtures of random walks. *Ecology*, **85**, 2436–2445.

Mueller, T. & Fagan, W.F. (2008) Search and navigation in dynamic environments – from individual behaviors to population distributions. *Oikos*, **117**, 654–664.

Mueller, T., Fagan, W. & Grimm, V. (2011) Integrating individual search and navigation behaviors in mechanistic movement models. *Theoretical Ecology*, **4**, 341–355.

Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D. et al. (2008) A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences*, **105**, 19052–19059.

Ovaskainen, O. & Crone, E.E. (2010) Modeling animal movement with diffusion. *Spatial Ecology* (eds S. Cantrell, C. Cosner & S. Ruan). Chapman and Hall, London, UK.

Rettie, W.J. & Messier, F. (2000) Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. *Ecography*, **23**, 466–478.

Rolandsen, C.M.R., Solberg, E.J., Bjørneraas, K., Heim, M., Van Moorter, B., Herfindal, I. et al. (2010) Elgundersøkelsene i Nord-Trøndelag, Binal og Rissa 2005–2010 – Sluttrapport. NINA Rapport 588, Trondheim.

Stephens, D.W. & Krebs, J.R. (1986) *Foraging Theory*, 1st edn. Princeton University Press, Princeton, New Jersey, USA.

Therneau, T.M. & Grambsch, P.M. (2000) *Modeling Survival Data: Extending the Cox Model*. Springer, New York.

Tufto, J., Andersen, R. & Linnell, J. (1996) Habitat use and ecological correlates of home range size in a small cervid: the roe deer. *Journal of Animal Ecology*, **65**, 715–724.

Van Moorter, B., Visscher, D., Benhamou, S., Börger, L., Boyce, M.S. & Gaillard, J.M. (2009) Memory keeps you at home: a mechanistic model for home range emergence. *Oikos*, **118**, 641–652.

Van Moorter, B., Bunnefeld, N., Panzacchi, M., Rolandsen, C.M., Solberg, E.J. & Sæther, B.-E. (2013a) Understanding scales of movement: animals ride waves and ripples of environmental change. *Journal of Animal Ecology*, **82**, 770–780.

Van Moorter, B., Visscher, D., Herfindal, I., Basille, M. & Mysterud, A. (2013b) Inferring behavioural mechanisms in habitat selection studies getting the null-hypothesis right for functional and familiarity responses. *Ecography*, **36**, 323–330.

Van Moorter, B., Rolandsen, C., Basille, M. & Gaillard, J.-M. (2015) Data From: Movement is the glue connecting home ranges and habitat selection. *Dryad Digital Repository*, http://dx.doi.org/10.5061/dryad.58j2m.

Whittaker, R.H. (1960) Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs*, **30**, 279–338.

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Demonstration of the relationship between resource selection and available variation.

Appendix S2. Demonstration of the decomposition of spatial variation into between and within home range variation.

Appendix S3. Demonstration of the relationship between spatial autocorrelation, and between- and within-home range variation.

Appendix S4. Supplementary tables and figures.