

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

# Predicting the *continuum* between corridors and barriers to animal movements using Step Selection Functions and Randomized Shortest Paths

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## Summary

1. The loss, fragmentation and degradation of habitat everywhere on Earth prompts increasing attention to identifying landscape features that support animal movement (corridors) or impedes it (barriers). Most algorithms used to predict corridors assume that animals move through preferred habitat either optimally (e.g. least cost path) or as random walkers (e.g. current models), but neither extreme is realistic.

2. We propose that corridors and barriers are two sides of the same coin and that animals experience landscapes as spatiotemporally dynamic corridor-barrier *continua* connecting (separating) functional areas where individuals fulfil specific ecological processes. Based on this conceptual framework, we propose a novel methodological approach that uses high-resolution individual-based movement data to predict corridor-barrier *continua* with increased realism.

3. Our approach consists of two innovations. First, we use step selection functions (SSF) to predict friction maps quantifying corridor-barrier *continua* for tactical steps between consecutive locations. Secondly, we introduce to movement ecology the randomized shortest path algorithm (RSP) which operates on friction maps to predict the corridor-barrier *continuum* for strategic movements between functional areas. By modulating the parameter  $\Theta$ , which controls the trade-off between exploration and optimal exploitation of the environment, RSP bridges the gap between algorithms assuming optimal movements (when  $\Theta$  approaches infinity, RSP is equivalent to LCP) or random walk (when  $\Theta \rightarrow 0$ , RSP  $\rightarrow$  current models).

4. Using this approach, we identify migration corridors for GPS-monitored wild reindeer (*Rangifer t. tarandus*) in Norway. We demonstrate that reindeer movement is best predicted by an intermediate value of  $\Theta$ , indicative of a movement trade-off between optimization and exploration. Model calibration allows identification of a corridor-barrier *continuum* that closely fits empirical data and demonstrates that RSP outperforms models that assume either optimality or random walk.

5. The proposed approach models the multiscale cognitive maps by which animals likely navigate real landscapes and generalizes the most common algorithms for identifying corridors. Because suboptimal, but non-random, movement strategies are likely widespread, our approach has the potential to predict more realistic corridor-barrier *continua* for a wide range of species.

**Key-words:** bottlenecks, connectivity, gene flow, graph theory, green infrastructures, obstacles, permeability, space use, tactical and strategic movements

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## Introduction

Animal movements are driven by spatial and temporal heterogeneity in the distribution of areas suitable for activities such as feeding, resting, mating, raising newborns and escaping predators (De Jager *et al.* 2011; Van Moorter *et al.* 2013). Movement is essential for individual survival, for gene flow in metapopulations and for species' colonization of new areas. No less important, long-distance movements such as mass migrations count among the Earth's most spectacular and fascinating ecological phenomena, coupling ecological communities across the globe and influencing their diversity and resilience (Bauer & Hoyer 2014). However, migrations are also especially vulnerable to anthropogenic habitat loss and fragmentation and have, therefore, become an increasingly endangered phenomenon (Wilcove & Wikelski 2008; Harris *et al.* 2009). In addition to migration routes, an increasing number of smaller scale, daily movements are being intersected, hampered or blocked by human infrastructure and cause concerns for species conservation and human safety (e.g. wildlife-vehicle collisions). As a consequence, in recent decades, there has been a strong demand to prevent and mitigate the effects of fragmentation on species' conservation and to minimize human-wildlife conflicts. This is not an easy task. First, it entails a deeper understanding of the concepts of movement corridors (see review in: Hess & Fischer 2001). Secondly, it entails developing analytical tools to predict with higher realism the location of corridors and the consequences of possible mitigation/de-fragmentation actions and land-use plans on animal movements. Here, we propose a conceptual framework unifying previous definitions of corridors and barriers and then use it to develop a novel methodological approach for predicting probabilistically the corridor-barrier *continuum*.

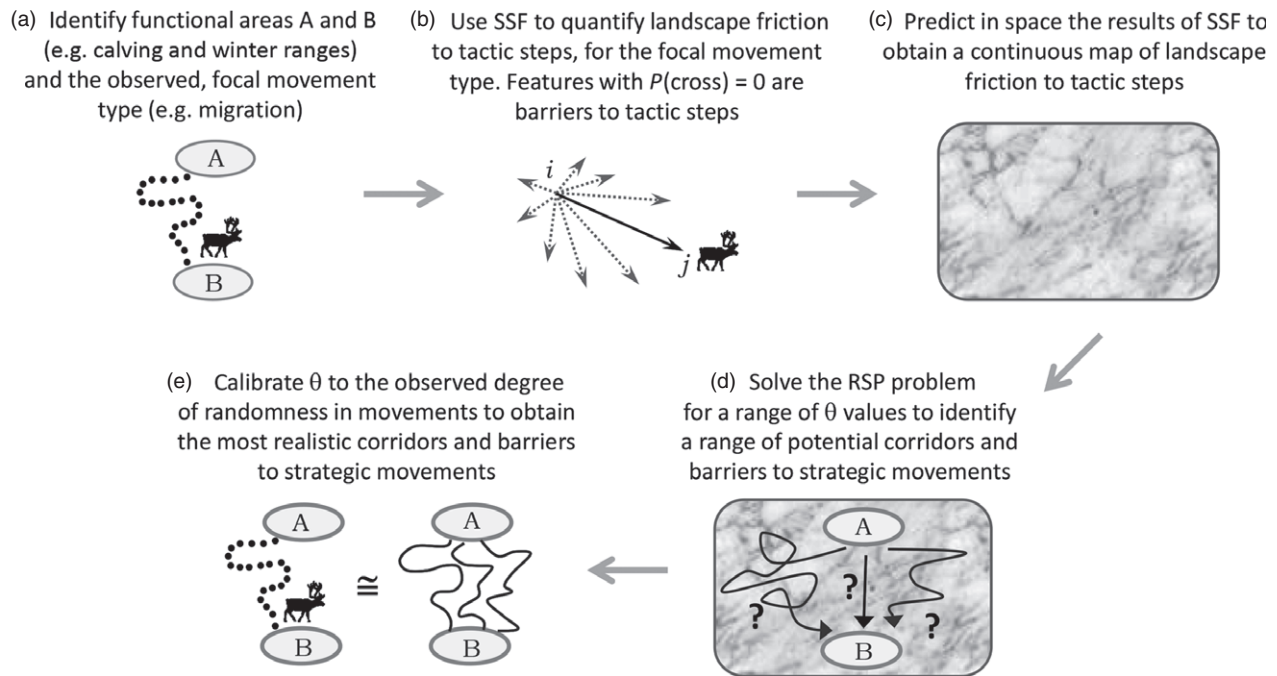
Over the past few decades, ecologists, managers and landscape planners have debated the definition of corridors based on attributes such as shape, size, length, habitat quality or animal movement patterns (see reviews by Tischendorf & Fahrig 2000; and Hess & Fischer 2001). One of the most recent and comprehensive definitions describes corridors as regions that facilitate the flow or movement of individuals, genes and ecological processes (Chetkiewicz, St. Clair & Boyce 2006; Hilty, Lidicker & Merenlender 2006). The term 'barrier' has been used to indicate both permeable and impermeable hindrances (Dyer *et al.* 2002; Holdo *et al.* 2011), or features that can or cannot be circumvented (Alerstam 2001; Beyer *et al.* 2015). We build on these concepts and study simultaneously corridors and barriers as a single, inextricable element shaping the distribution of individuals and species at multiple scales.

For a given ecological process (e.g. migration, feeding) requiring movement between two or more areas that provide specific resources at specific times (hereafter 'functional areas', Panzacchi *et al.* 2010), we define 'corridors' as areas through which genes, individuals or populations

flow, and 'barriers' as areas that impede such flow. This definition implies that corridors and barriers stand at the opposite ends of a *continuum* in which barriers can originate by decreasing the width of passageways (Ovaskainen & Crone 2010) or by increasing their length or decreasing their permeability above a threshold (e.g. Skogland 1986). Alternatively, both non-traversable natural or man-made features, such as cliffs or fences, and non-traversable areas, such as oceans, can act as barriers (e.g. Gill *et al.* 2009). The proposed definition also implies that a home range can be viewed as an assemblage of spatiotemporally dynamic functional areas connected (or separated) by spatiotemporally dynamic corridors (or barriers). Finally, our definition implies that corridors can be characterized by any shape and size, be diffused or demarcated, composed of good- or poor-quality habitat, and suitable or unsuitable for survival, growth and reproduction, as long as they allow for the focal movements between functional areas. Note that we did not define observed corridors as area *units* with the highest *probability* of being traversed, as such a definition would equate corridors to bottlenecks and may, thus, overlook wider and more ecologically relevant connectivity areas.

By defining corridors and barriers to movements within the same conceptual framework, we set the basis for developing a matching analytical framework to identify both features simultaneously. Imagine the path followed by water drops flowing from a mountaintop to the sea. The drops have to circumvent a long series of small obstacles such as boulders in the river bed and can eventually reach the sea only if no impermeable obstacles, such as dams or deserts, impede the flow. In movement ecology, goal-oriented and often far-reaching movements are called 'strategic' and can be broken down into a series of opportunistic and often short-term 'tactical' steps (Gaustad & Myrsetrud 2005). Accordingly, the process of identifying corridors is usually broken down into a first phase quantifying permeability at the step scale *i-j* (or, by analogy, identifying the river bed and boulders therein; Fig. 1b,c) and into a second phase focussing on the completion of the entire movement flow from a starting area *A* to a destination *B* (or, identifying dams and deserts; Fig. 1d,e). The analytical approach we propose attempts to improve both stages and, thus, aims at identifying corridor-barrier *continua* with increased realism with respect to available approaches.

Step-scale permeability is typically represented by friction maps, which are intended to represent the animals' reluctance or failure to traverse a given landscape unit based on willingness, capabilities and physiological costs (Sawyer, Epps & Brashares 2011). In the landscape-connectivity literature, friction is usually calculated as the inverse of the probability of habitat use or selection, based on the assumption that these metrics reflect the species' willingness and ability to traverse a given spatial unit (review: Zeller, McGarigal & Whiteley 2012). This is, however, a strong assumption, because preferred habitat



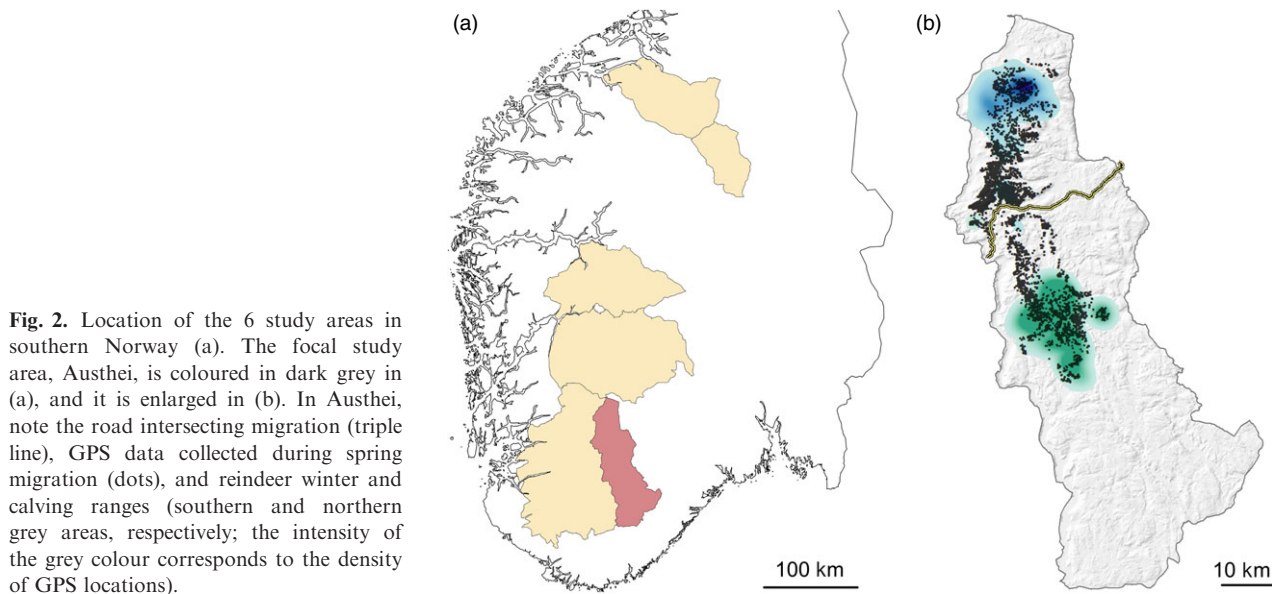
**Fig. 1.** Illustration of the analytical steps used to predict a realistic corridor-barrier continuum using step selection functions (SSF) and randomized shortest path (RSP). Steps b–c quantify the probability of perform tactical movements between two consecutive GPS locations  $i$  and  $j$ , while steps d–e quantify the probability of the entire strategic movement from A to B.

may not be traversable due to fences or, conversely, poor-quality habitat, such as road underpasses, may represent preferred pathways. Indeed, Zeller, McGarigal & Whiteley (2012) concluded that there is a widespread tendency to confound movement behaviour and resource use in studies estimating landscape resistance to movements. Here, we suggest using high-resolution animal movement data to calculate friction as the inverse of the probability to traverse each spatial unit, without necessarily relying on untested assumptions on habitat preferences. Specifically, we suggest using step selection functions to estimate directly the probability of each observed step to cross a range of spatial features (Fortin *et al.* 2005; Thurfjell, Cuiti & Boyce 2014; Fig. 1a).

In the second stage, friction maps serve as input for a range of algorithms used, in turn, to predict the strategic path followed by animals moving between functional areas. The most common algorithms either identify optimal travel routes or identify corridors as emergent properties of movement characteristics. Optimization approaches such as the least cost path or network models (Pinto & Keitt 2009; Carroll, McRae & Brookes 2012) assume that animals have a complete knowledge of the landscape and identify the optimal route with regard to criteria such as length and habitat quality. By contrast, movement-based approaches (e.g. current models, McRae *et al.* 2008; agent-based models, Tang & Bennett 2010; diffusion models, Ovaskainen *et al.* 2008) assume only knowledge of the immediate surroundings and simulate movements mechanistically, usually via random walks (Pearson 1905). Hence, while optimization approaches allow predicting

corridors similar to those used by animals moving optimally ‘as the crow flies’, algorithms based on random walk (also known as ‘the drunkards’ walk’) highlight trajectories similar to those used by animals walking randomly. We hypothesize that both assumptions of optimal and random movements are rarely met by animals, which most often make iterative movement decisions trading off exploration and optimal exploitation of the environment. Based on these premises, we introduce a novel algorithm to movement ecology, the randomized shortest path, RSP (developed in Saerens *et al.* 2009; and Kivimäki, Shimbo & Saerens 2014), which models the actual degree of randomness in animal movements. Calibration of the RSP  $\theta$  parameter makes it possible to maximize model agreement with observed movement patterns, and the best fitting model is then used to predict corridors. Thus, RSP bridges the gap between optimization and random walk-based approaches, and it has the potential to highlight more realistic movement corridors compared to optimization or movement-based approaches (Fig. 1d).

We integrate these two stages – identification of tactical steps via SSF and identification of strategic paths via RSP – to offer a more holistic and evidence-based approach to the study of corridors and barriers (Fig. 1). We illustrate the proposed framework by focusing on *Rangifer t. tarandus* in Norway, which hosts the last remaining populations of wild mountain reindeer. Before industrial development, intermixing herds of wild reindeer exhibited massive seasonal migrations between adjacent mountain systems (Panzacchi, Van Moorter & Strand 2013b). Today, largely due to the development of infrastructure,



**Fig. 2.** Location of the 6 study areas in southern Norway (a). The focal study area, Austhei, is coloured in dark grey in (a), and it is enlarged in (b). In Austhei, note the road intersecting migration (triple line), GPS data collected during spring migration (dots), and reindeer winter and calving ranges (southern and northern grey areas, respectively; the intensity of the grey colour corresponds to the density of GPS locations).

reindeer can no longer follow most of their traditional migration routes and are virtually isolated as more than 20 unique subpopulations. One of the last remaining migrations can be observed in the Austhei subpopulation, where reindeer move seasonally ca. 60 km between non-overlapping winter and calving grounds separated by a road paralleled by a hydropower reservoir and mountain cabins (Fig. 2). Previous studies concluded that the disturbance associated with these developments hamper spring migration and may delay reindeer arrival at the calving ground (Panzacchi, Van Moorter & Strand 2013a). We illustrate the conceptual and methodological framework we advocate above to a large data set of GPS data from the Austhei reindeer subpopulation to (a) identify probabilistically both the steps and paths that comprise the entire migration corridor between winter and calving ranges and (b) identify the locations where migratory routes are most likely to intersect built infrastructure.

## Materials and methods

### REINDEER RANGES AND GPS DATA

The study is based on GPS locations taken from 186 reindeer females from six of the largest populations (Austhei, Ryfylke, Hardangervidda, Nordfjella, Rondane and Snøhetta) scattered throughout the distribution range, in Norway, from 2001 to 2012 (Fig. 2). These data (one location every 3 h for each individual) were used to estimate landscape permeability. In addition, we focused on the south-eastern population of Austhei to predict the location of the corridor-barrier *continuum* to migration. This population inhabits the homonymous wild reindeer management area in the southernmost part of the range in Norway (7°78'E, 59°23'N) and migrates from winter ranges in the north to calving areas in the south by crossing a 50-km segment of a road (Fig. 2). The average daily traffic on this road is low, but it increases during Easter holidays, which most often coincide with the spring migration period. In Austhei, we collected GPS data for nine females from 2007 to 2012. In addition to standard data collection (1 loc./3 h), we

followed an intensive sampling schedule (1 loc./15 min) in proximity of the road to quantify crossing locations more precisely. Based on previous studies (Panzacchi, Van Moorter & Strand 2013b) quantifying migration statistics using the net squared displacement approach (Bunnefeld *et al.* 2011), we selected locations from April 10 to May 20 to represent the migration period. Based on calving dates estimated using movement statistics as described in Panzacchi, Van Moorter & Strand (2013b), we selected locations from May 15 to May 31 to represent the calving range. Locations from January were used to represent the winter range (Fig. 2). Descriptions of the study areas, capture methods and data-handling procedures are provided by Panzacchi, Van Moorter & Strand (2013b) and Panzacchi *et al.* (2015a,b).

### USE OF STEP SELECTION FUNCTIONS TO PRODUCE FRICTION MAPS

Figure 1 illustrates the analytical steps used to identify the corridor-barrier *continuum* for animals starting in functional area *A* and moving to a destination *B*. After defining the focal ecological process in time and space (i.e. migration timing and seasonal ranges), as explained above, we used a step selection function (SSF, Fortin *et al.* 2005) to quantify the probability of each landscape feature being crossed by a step *s* from *i* to *j* (Fig. 1b). We compared the characteristics of the landscape traversed by each observed step *s<sub>m</sub>* to those of 10 potentially available random steps *s<sub>mr</sub>* using conditional logistic regression, CLR. For this analysis, we used all available GPS data during spring migration from all study areas (114/individuals/year) and extracted an equal number of steps among study areas (total number of steps *M* = 30410 steps). Random steps *s<sub>mr</sub>* were generated by associating a random end location *j*<sup>\*</sup> to the starting location *i* from the observed step *s<sub>m</sub>*. Because choosing end locations *j*<sup>\*</sup> that are too close to the observed starting location *i* would lead to the risk of overlooking features that induce avoidance (Zeller, McGarigal & Whiteley 2012), we sampled *j*<sup>\*</sup> according to a uniform *SL* distribution, in which the maximum *SL* corresponded to the 99% percentile of the observed *SL* (3 km); turning angles were chosen randomly.

The parameters in the SSF were estimated by maximizing the following likelihood function:



$$L(\beta, s) = \prod_{m=1}^M \frac{f(\underline{x}(s_m), \beta)}{\sum_{r=1}^{10} f(\underline{x}(s_{mr}), \beta)} \quad \text{eqn 1}$$

where  $\underline{x} = \{x_1, x_2, \dots, x_p\}$  are  $p$  covariates associated with each step, and  $\beta = \{\beta_1, \beta_2, \dots, \beta_p\}$  are the maximum likelihood coefficients estimates. The SSF has the following structure:

$$f(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \dots + \beta_{p-1} x_{p-1} + \beta_p g(asL)) \quad \text{eqn 2}$$

where the function  $g$  is a spline on the adjusted step length  $asL$  associated with the step. To increase accuracy in the step length estimation,  $SL$  (linear  $i$ - $j$  distance) was adjusted to account for topographic variations along the step using a digital elevation model, DEM:

$$asL = \sum_{i=1}^{k-1} \sqrt{(DEM_{i+1} - DEM_i)^2 + \left(\frac{SL}{k-1}\right)^2} \quad \text{eqn 3}$$

where  $k$  = total number of 25-m pixels traversed by the step (leaving unchanged steps smaller than a pixel, i.e. when  $k = 1$ ). By dividing the  $SL$  in  $k-1$  pieces, we ensured that  $asL = SL$ ,

**Table 1.** List covariates used in the step selection function. Each covariate, measured along each observed and random step  $i$ - $j$ , was measured at 100 m resolution. The land cover map was provided by Johansen 2009, and all other layers were derived from [www.geonorge.no](http://www.geonorge.no)

Covariate	Metric calculated along the step $i$ - $j$
Step length (corrected)	Distance, corrected for changes in elevation
Max slope	Maximum slope (from D.E.M.), squared
Max solar radiation	Max. solar radiation (proxy of snow-free areas)
Max trail density	Max. density (calculated within 1 km) of skiing trails
Max road density	Max. density of public and private roads (as above)
Max rail density	Max. density of railways (as above)
Max tourist cabin	Max. density of tourist cabins, D.N.T. (as above)
Max private cabin	Maximum density of private cabins (as above)
Road crossing	Binary variable indicating whether $i$ - $j$ crossed a road
Trail crossing	Binary variable indicating whether $i$ - $j$ crossed a trail
Railway crossing	Binary variable indicating whether $i$ - $j$ crossed a railway
LC: forest veg.	Proportion of Land Cover * class: forest vegetation
LC: bog	Prop. of LC: bog
LC: mountain edible veg.	Prop. of LC: mountain veg. edible for reindeer in spring
LC: mountain not edible veg.	Prop. of LC: other mountain vegetation
LC: fields	Prop. of LC: fields
LC: urban areas	Prop. of LC: urban areas
LC: natural lakes	Prop. of LC: non dammed lakes
LC: reservoirs	Prop. of LC: dammed lakes

\*The land cover classes identified by Johansen 2009 were grouped into 8 classes of relevance for reindeer during spring.

when  $(DEM_i - DEM_{i-1})^2$  equals 0. Fortin *et al.* (2005) selected random step based on the observed  $SL$  distribution. However, according to Forester, Im & Rathouz (2009), this would lead to biased estimates of the  $\beta$  in (eqn 2), because the observed  $SL$  distribution is the result of both habitat-independent movement kernel and habitat selection. Hence, we followed Forester, Im & Rathouz (2009) and used  $SL$  as a covariate in the analysis, which leads to less biased estimates. Along each observed and random step, we measured 19 covariates ( $x_1$  to  $x_p$ ) using a set of metrics described in Table 1. In particular, we calculated the following: (i) the maximum value traversed by a step, for continuous covariates; (ii) the proportion of each class traversed by a step, for categorical variables; and (iii) a binary variable indicating whether a step crossed a linear feature. The covariates, which were measured at 100 m resolution, indicated both environmental variables and human infrastructures; the latter were represented both by linear features (e.g. roads) and by maps quantifying the density of a given type of infrastructure calculated within 1 km radius, to allow SSF to detect proximity-related avoidance effects. Using the estimates from (eqn 2), we predicted the cost-of-movement map **C** (or 'friction map') in a discretized space (i.e. lattice) based on the environmental layers describing the area (Fig. 1c), as follows:

$$c_j = 1/\text{logit}^{-1}(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \dots + \beta_p x_p) \quad \text{eqn 4}$$

where  $\beta_1$  to  $\beta_p$  are the coefficients estimated by CLR in (eqn 2), and  $x_1$  to  $x_p$  are the covariate characteristics associated with each pixel  $j$  on the map. In other words, we predicted the probability of each pixel being crossed based on the landscape features therein. Note that in CLR, as in all other Resource Selection Functions, no intercept  $\beta_0$  is estimated. In other words, the model yields values proportional, but not equal, to the probability of use of a resource unit; and therefore, the baseline friction of the landscape is unknown. After testing for a range of values, we selected  $\beta_0 = -4$ , which allowed us to obtain the most realistic estimates of the ability and willingness of reindeer to traverse available landscape features in southern Norway during spring.

#### RANDOMIZED SHORTEST PATH TO PREDICT THE CORRIDOR-BARRIER CONTINUUM

After quantifying friction to steps  $i$ - $j$ , we needed to estimate, for each pixel  $j$ , the expected number of passages,  $\bar{n}_j$ , of animals moving between functional areas **A** and **B**. This problem is usually solved in the following way. First, the problem is discretized and a sufficiently dense grid is defined based on the map of the area, providing a graph or network on which the animal can move from node  $i$  to node  $j$  by following edges or links (Urban *et al.* 2009). A cost  $c_{ij}$  is associated with the edges to quantify the difficulty of moving along the edge from node  $i$  to  $j$  (which, in our approach, was simplified to the cost of moving 'into' node  $j$ , i.e.  $c_{ij} = c_j$ ; see Appendix S1, Supporting information for details). Secondly, the animal has to choose a strategy for reaching area **B** from area **A**. Two such common strategies are the shortest path, or geodesic, strategy (e.g. Cormen *et al.* 2009) and the pure random walk (e.g. Doyle & Snell 1984). Because we hypothesized that animals often balance between exploitation (minimizing total cost along the trajectory) and exploration (exploring neighbouring nodes), we chose to use RSP (Saerens *et al.* 2009; Kivimäki, Shimbo & Saerens 2014), which defines a trade-off between fol-

lowing the shortest path and performing a random walk. The resulting strategy defines a biased random walk in which the animal is 'attracted' by the destination node. The RSP model estimates, for each pixel  $j$ , the expected number of passages,  $\bar{n}_j$ , of animals moving from node 1, located in area  $A$ , to node  $n$  in area  $B$  as a function of the cost matrix  $C$  (i.e. friction map, eqn 4) and of the parameter  $\Theta$ . The parameter  $\Theta$  modulates the balance between exploitation and exploration. For larger  $\Theta$  values, RSP performs like an optimization method, equivalent to least cost path. When  $\Theta = 0$ , RSP behaves like a random walk-based approach, equivalent to current models. Note that the magnitude of  $\Theta$  depends on the size of the graph and on the average cost of the friction map  $C$ ; in particular, for small graphs with low cost  $\Theta \rightarrow \infty$ . For each pixel  $j$ , RSP computes the expected number of passages,  $\bar{n}_j$ , over all paths between nodes 1 and  $n$  (where  $n$  is absorbing) as follows:

$$\bar{n}_j = \frac{z_{1j}z_{jn}}{z_{1n}} \quad \text{eqn 5}$$

where the matrix  $Z$  is derived from the cost matrix  $C$  with cost  $c_{ij}$ , and  $\theta$ , as follows:

$$Z = (I - P \circ \exp[-\theta C])^{-1} \quad \text{eqn 6}$$

where  $\circ$  is the elementwise (i.e. Hadamard) matrix product.  $I$  is the identity matrix, and  $P$  is the transition matrix, where: for  $i \neq n$ ,  $p_{ij} = c_{ij}^{-1} / \sum_{j=1}^n c_{ij}^{-1}$ , and  $p_{nj} = 0$  for all  $j$  (the larger the cost, the lower the probability of following this link). Note that  $p_{ij}$  and  $c_{ij}$  are the entries of the matrices  $P$  and  $C$ , respectively. A detailed description of the RSP is provided in Appendix SI (Supporting information) and references therein. The RSP model was computed using the function 'PASSAGE' in the R package 'GDISTANCE' (Van Etten 2012; see also Van Etten & Hijmans 2010).

We used RSP to predict the corridor-barrier *continuum* for the spring migration performed by the Austrei reindeer population. First, we paired 100 points sampled randomly within each of the winter and calving areas (Fig. 2). We then computed the RSP model for each pair, based on the tactical-movement friction map produced by the SSF. Finally, we computed the mean of the values  $\bar{n}_j$  over the 100 node pairs to estimate the overall number of visits to node  $j$  when moving from the winter area to the calving area. The RSP model was computed for  $\theta$  values ranging from 0 (i.e. random movements) to 0.1 (i.e. shortest path):  $\Theta = 0$ ,  $\Theta = 1e-6$ ,  $\Theta = 5.5e-6$ ,  $\Theta = 1e-5$ ,  $\Theta = 1e-4$ ,  $\Theta = 1e-3$ ,  $\Theta = 0.1$ .

#### CALIBRATION OF THE CORRIDOR-BARRIER CONTINUUM

We calibrated the RSP  $\Theta$  parameter to maximize model agreement with respect to observed corridors. Observed corridors were identified using Brownian bridge movement models (Horne *et al.* 2007) using 1 loc./15 min. for 10 individuals/year. When the intensive sampling scheme was not available, the standard data set (1 loc./3 h, 22 individuals/year) was used instead. We compared the agreement between predicted and observed corridors in two ways; by comparing the predicted (from RSP) and observed (from Brownian bridges) utilization distributions UD<sub>s</sub> during migration and along the road intersecting migration. First, to ensure that all individuals had the same weight, individual UD<sub>s</sub> were cropped to the same extent and rescaled to sum to one. We

then summed all individual UD<sub>s</sub> to identify population-scale migration corridors, and we rescaled it to sum to one, to allow for comparison with the predictions. We then identified the best fitting  $\Theta$  parameter by comparing predicted and observed UD<sub>s</sub>. Although there are several metrics to quantify similarities between UD<sub>s</sub> (e.g. Fieberg & Kochanny 2005), we were more interested in quantifying dissimilarities, and therefore, we compared observed and predicted UD<sub>s</sub> using the mean squared error, MSE, that penalizes large deviations. In addition, for each individual, we intersected the UD with the road to quantify the probability of crossing at different locations. As before, individual probabilities were rescaled, summed to obtain a population-level probability distribution of crossing the road, and the sum was rescaled. We used a 1 km moving average to aggregate road crossing probabilities over 100 m road segments. The best fitting  $\Theta$  parameter was then found by minimizing the MSE of the crossing probabilities (Fig. 5).

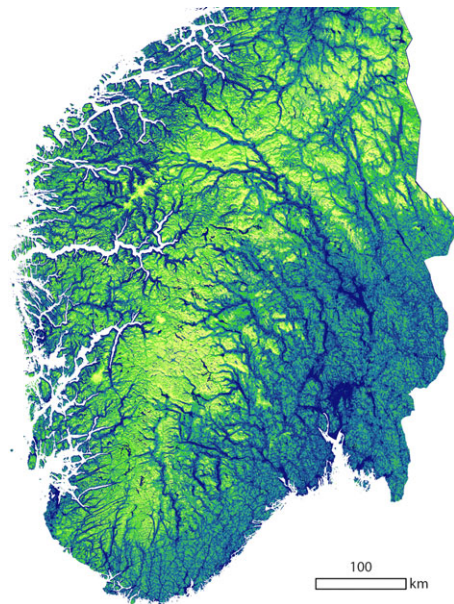
All analyses were conducted in R Core Team (2013), and the codes to perform the analyses are provided in Appendix S2 (Supporting information).

## Results

The probability of taking a given step decreased nonlinearly with maximum slope, with maximum trail and road density and with the presence of a road intersecting the step (Table 2). We detected a positive effect on taking a step for mountain vegetation, particularly edible species, and of solar radiation, whereas there was a negative effect from the proportion of bogs and lakes negatively. Inter-

**Table 2.** Variables included in the most parsimonious step selection function model, which indicate the probability of a reindeer step traversing each habitat feature. Model prediction is shown in Fig. 1b

Covariate	Coef	SE(coef)	Chisq	DF	P
Step length (corrected), linear	-7.630e-04	1.69e-05	2041.51	1.00	<0.001
Step length (corrected), nonlinear			9698.03	1.09	<0.001
(Max slope) <sup>2</sup>	-1.113e-03	3.48e-05	1021.12	1.00	<0.001
Max trail density	-1.381e-01	2.31e-02	35.71	1.00	<0.001
Max road density	-5.260e-01	1.01e-01	27.38	1.00	<0.001
Max solar radiation	3.889e-01	1.06e-02	1351.02	1.00	<0.001
LC: bog	-4.978e-01	1.56e-01	10.13	1.00	<0.001
LC: mountain not edible veg.	1.710e-01	6.90e-02	6.14	1.00	<0.05
LC: mountain edible veg.	5.987e-01	6.11e-02	96.14	1.00	<0.001
LC: natural lakes	-1.326e+00	1.26e-01	110.03	1.00	<0.001
LC: reservoirs	-3.875e+00	4.65e-01	69.51	1.00	<0.001
Road crossing	-3.556e-01	1.27e-01	7.78	1.00	<0.05



**Fig. 3.** Friction map illustrating the gradient between pixels that can be traversed more easily (lightest areas) and those that cannot be traversed (i.e. barriers to tactical steps; darkest areas) by each reindeer step (i.e. consecutive locations) during spring migration. The map was produced by predicting in space the results of a step selection function used to quantify landscape friction to the movements of 186 GPS-monitored reindeer from six study areas across the distribution range, in Norway. Note that the barriers identified largely correspond to the boundaries of the study area shown in Fig. 2.

estingly, the probability of crossing natural lakes was much higher (24%) than the probability of crossing reservoirs (2%), potentially due to their less reliable ice cover. The spatial prediction of the SSF (Fig. 3) illustrates the gradient in landscape friction to tactical movements. Features with probability of crossings = 0, such as railways, represent impermeable barriers to tactical steps (darkest areas in Fig. 3). Figure 3 shows that most reindeer management areas are delimited by high-friction areas, largely due to the presence of infrastructures or, in some cases, of topographic barriers such as steep mountains and fjords.

Given the size of our grid and its associated movement costs,  $\Theta$  ranged between 0 (representing a random walk) and 0.1 (approaching the least cost path). We run seven RSP models with  $\Theta$  values included between these extremes, and we illustrate the results of three of the models in Fig. 4. The model with  $\Theta = 1 \times 10^{-5}$  minimized the mean squared error of the difference between predicted and observed corridors estimated by the sum of Brownian bridge movement models (Table 3) and therefore best predicted the location of the entire migration corridor (Fig. 5a). The same model ( $\Theta = 1 \times 10^{-5}$ ) also minimized the mean squared error of the difference between predicted and observed road crossing locations (Table 3) and therefore provided the most realistic predictions of road locations where reindeer crossings occurred (Fig. 5b).

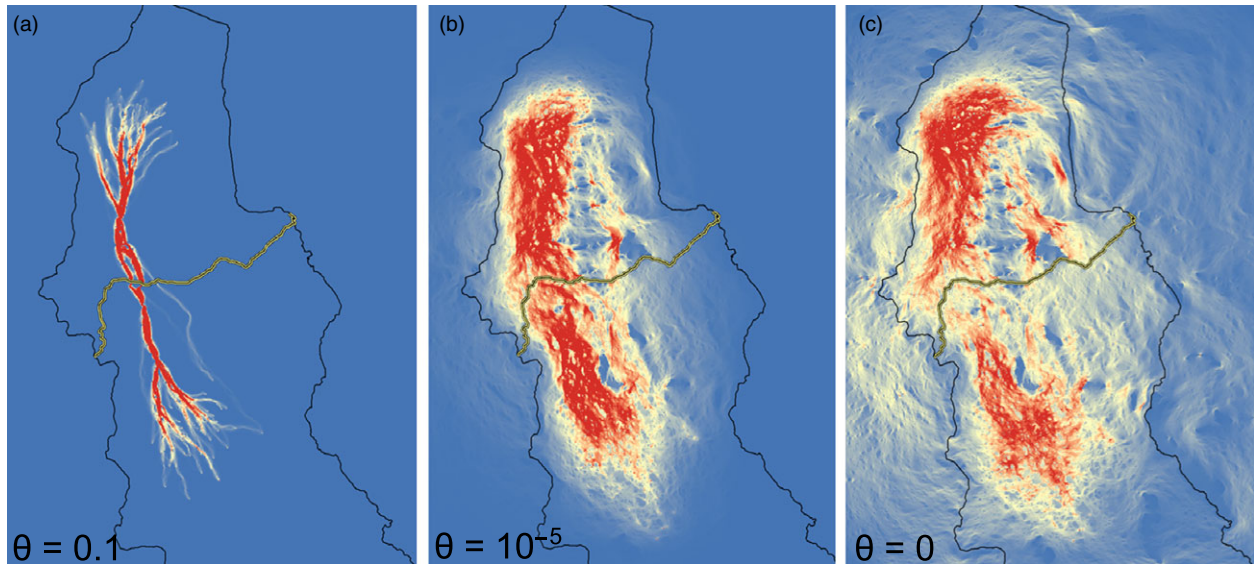
## Discussion

Having defined corridors and barriers as two sides of the same coin, which allow or prevent movements at specific spatio-temporal scales, we establish a methodological approach for quantifying the corridor-barrier *continuum* for both tactical and strategic movements. The approach presents two innovations. First, the use of step selection functions to predict spatially explicit friction maps that quantify step-based landscape permeability. Secondly, the use of randomized shortest path to predict corridors and barriers for movement strategies ranging from optimal to random. By applying this framework to wild reindeer in Norway, we identified probabilistically the corridor-barrier *continuum* that most closely fits empirical data both during the entire migration and, at a finer spatial scale, along the road intersecting it (Fig. 5).

Model calibration demonstrated that the movement paths predicted by the RSP model fit the data better compared to alternative approaches relying on assumptions of either optimality or random walk and therefore showed that reindeer migrate with intermediate movement strategies trading off optimization and exploration at every step. Because both perfectly optimal and fully random movement strategies are likely to be widespread across species, RSP can help identify more realistic movement corridors and barriers for a range of animals, plants and genes (see Van Etten & Hijmans 2010).

Recent review papers stress the importance of reliable friction maps for the identification of realistic corridors and provide recommendations for improving the estimation of permeability. In particular, several authors invoked a deeper understanding of the link between fine-grain habitat use and movements and warned against the tendency to confound movement behaviour and resource use (Sawyer, Epps & Brashares 2011; Zeller, McGarigal & Whiteley 2012; Potts *et al.* 2014). We support these suggestions and propose using SSF to quantify directly fine-scale friction for tactical steps to generate friction maps. SSFs can be very powerful tools for producing friction maps because they compare directly landscape characteristics encountered along each step to those the animal would have encountered if choosing a random alternative. Note, however, that to estimate step-based crossing probabilities, it is essential to consider landscape characteristics measured *along* each step, rather than at the start and endpoint of it. Hence, particular attention should be paid to the calculation of ecologically relevant metrics along the step and to the intersection between steps and linear features that may act as potential barriers. If topography is likely to affect step selection for the species of interest, precision in the estimates of step-based crossing probabilities can be increased by adjusting the step length to account for changes in elevation, as we did. The results of the SSF support previous studies indicating reindeer avoidance to a series of infrastructures (Panzacchi, Van Moorter & Strand 2013a; Beyer *et al.* 2015; Panzacchi





**Fig. 4.** Three predictions of the *continuum* between corridors (red to cream) and barriers (cream to blue) to spring migration in Austheia (see Fig. 1) based on randomized shortest path models with  $\Theta$  values ranging between  $\Theta = 0.1$  (i.e. assuming fully optimal movements, as in least cost path; panel a) and  $\Theta = 0$  (i.e. assuming fully random movements, as in current models; panel b). Panel c illustrates the best fitting model, with  $\Theta = 1 \times 10^{-5}$ . The road intersecting migration is outlined in yellow.

**Table 3.** Calibration of the RSP  $\Theta$  parameter to identify the model that best fits the empirical data. The calibration was performed by comparing agreement between the utilization distribution of observed corridors (calculated using Brownian bridge movement models) and of seven predicted corridors (calculated using RSP with  $\Theta$  ranging between 0, as in current models, and 0.1, as in least cost paths; first column). The agreement was quantified using the mean squared error (MSE) at two spatial scales: across the entire migration and along the road intersecting migration (see Fig. 5). Lower MSEs indicate better agreement between predicted and observed corridors

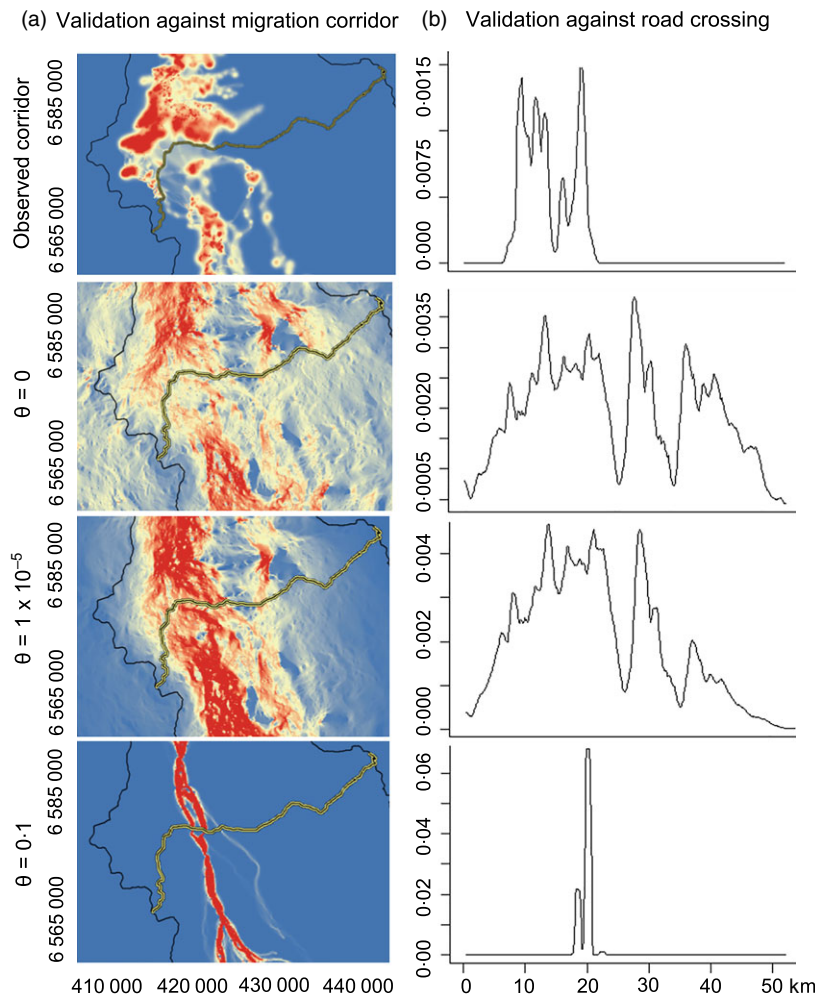
RSP model - $\Theta$	MSE – Migration	MSE – Road crossing
0 (~ current model)	$1.040 \times 10^{-9}$	$1.293 \times 10^{-5}$
$1 \times 10^{-6}$	$1.024 \times 10^{-9}$	$1.176 \times 10^{-5}$
$5.5 \times 10^{-6}$	$1.013 \times 10^{-9}$	$1.072 \times 10^{-5}$
$1 \times 10^{-5}$	$1.009 \times 10^{-9}$	$1.028 \times 10^{-5}$
$1 \times 10^{-4}$	$1.015 \times 10^{-9}$	$0.892 \times 10^{-5}$
$1 \times 10^{-3}$	$1.171 \times 10^{-9}$	$1.545 \times 10^{-5}$
0.1 (~least cost path)	$3.541 \times 10^{-9}$	$8.332 \times 10^{-5}$

*et al.* 2015a,b) and quantify the permeability of those features. Additional improvements to the SSF framework can be envisioned. For example, Beyer *et al.* (2015) estimated each of movement parameters, habitat preferences and permeability of barriers within the same modelling framework, but at this stage, this approach may be computationally challenging for large data sets. Additionally, S. Lele, H. Beyer and some of the authors are developing step selection probability functions, yielding values not only proportional but equal to the probability of use.

To obtain more realistic predictions of movement corridors and barriers, we recommend a higher focus on the assumptions underlying the algorithms used. The assumptions that animals move either optimally (as in LCP) or randomly (as in Current Models) might be approximately

met, for example, in long-distance migrations or for animals roaming through novel landscapes. In most cases, however, these assumptions are unrealistic, and combining different approaches is often recommended (McRae *et al.* 2008; Howey 2011). The RSP algorithm bypasses these issues and bridges the gap between optimization and random walk-based assumptions through the parameter  $\Theta$ , which controls the trade-off between exploration and optimal exploitation of the environment (when  $\Theta \rightarrow \infty$ , RPS  $\rightarrow$  LCP; when  $\Theta \rightarrow 0$ , RSP  $\rightarrow$  current models). Effectively, RSP assumes that animals have a priori knowledge of the entire landscape, but, on one side, their movements are subject to some degree of randomness, and, on the other, they decide to sacrifice complete optimality for exploring the environment. These assumptions appear to be supported in our case study. Reindeer have prior knowledge of the functional areas used every year as seasonal ranges. In addition, our best fitting model shows that reindeer neither migrate optimally following the shortest path (see also Pullinger & Johnson 2010) nor do they move entirely at random, but they perform frequent exploratory movements. This is likely due to both some intrinsic level of randomness in individual behaviour and environmental stochasticity. In our case, it is interesting to note that the exploration appeared to be particularly marked in proximity to the road intersecting the migration route, whereas more directed movements occurred before and after crossing (unfortunately, the relatively small spatial scale did not allow testing for differences). These results support previous studies demonstrating the hampering effect of that road, which affects the animals' step length, net squared displacement, and seem to delay the arrival at the calving range (Panzacchi, Van Moorter & Strand 2013a; see also Sawyer *et al.* 2013).





**Fig. 5.** Calibration of the RSP  $\theta$  parameter to identify the best fitting predicted corridor-barrier *continuum* in Austhei. Figures in panel a compare observed corridors (represented by the utilization distribution, UD, from Brownian bridge movement models; top figure), to predicted corridors calculated using RSP with increasing  $\theta$  values. Figures in panel b compare the observed road crossing frequencies (calculated by intersecting the above described UD with the road) to those predicted by models with increasing  $\theta$  values. Only three RSP models are visualized:  $\theta = 0$  (current model),  $\theta = 1 \cdot 10^{-5}$  (best fitting model) and  $\theta = 0.1$  (least cost path). Note that figures in panel a show a close up around the road of the study area in Fig. 4 and note different scales on the y-axes in panel b.

We defined corridor-barrier *continua* with respect to given ecological processes occurring at specific spatiotemporal scales. In line with this framework, our methodological approach allowed identifying the corridor-barrier *continuum* for a specific ecological process and spatiotemporal scale. Hence, the areas identified as corridors in Fig. 5 are expected to act as such during spring migration, but may not be traversable in other seasons, or may be irrelevant for other ecological processes such as gene flow. Such transient windows of connectivity are common in dynamic environments (Zeigler & Fagan 2014), and understanding their spatiotemporal dynamics will undoubtedly increase management options for mitigating human–wildlife conflicts. For example, reindeer migration might be facilitated by minimizing human activity in specific areas along the road as reindeer approach, whereas no restrictions may be required in different areas and periods. Furthermore, we defined corridor-barrier *continua* only with respect to observed animal movement choices and capabilities, regardless of assumptions on movement patterns or landscape characteristics. In line with this framework, our methodology allowed identifying the most realistic corridors by modelling movement patterns similar to those exhibited by the species intent in the focal

ecological process, that is migration. In other words, model calibration plays a crucial role for the identification of the most likely *predicted* corridors, which are simply those more closely matching *observed* corridors – irrespective from their habitat quality, shape, size or other characteristics. Note that, in our case, the calibration process (i.e. computing seven models connecting 100 pairs of locations on a raster of 550 000 pixels, 100 m resolution) occupied a standard desktop computer for about a week. Some of the authors are developing a maximum likelihood method for tuning  $\theta$  more efficiently and robustly, based on the observed cost of trajectories between two locations.

Another approach to model the separate effects of directed and random movement is the use of advection–diffusion equations, where the diffusion corresponds to the random component and the advection to a directed component of RSP (Ovaskainen & Crone 2010; Moorcroft & Lewis 2006). Diffusion models have been used to model movements in heterogeneous landscapes (Ovaskainen & Crone 2010), to quantify functional connectivity (e.g. the effect of corridors on butterfly dispersal, Ovaskainen 2008) and to model detailed behavioural processes that structure movements (e.g. territorial scent marking, Moorcroft, Lewis & Crabtree 2006). In all of

these applications, the diffusion component is an uncorrelated limit of underlying correlated movements (partly a consequence of modelling much coarser data), and the advection term is generally applied to homogenous processes such as the dominant wind direction or a distance-dependent attraction to a home range centroid. One of the main innovations in the RSP formulation is in the inclusion of 'absolute spatial awareness', which models the cognitive maps by which animals likely navigate. In addition, RSP is 'globally optimal', in the sense that the expected cost to reach a destination (exploitation) is minimized subject to a given level of entropy (exploration). In other words, the outcome of RSP is always a 'least cost path' subject to a given level of randomness (controlled by  $\Theta$ ); to the best of our knowledge, such optimality guarantee does not exist in advection–diffusion models. In principle, the reformulation of RSP models to advection–diffusion models may be possible by redefining the advection term in terms of the LCP; this could be a subject for future research (E. Guraire, *personal communication*).

Over the past decades, the focus on movement corridors has increased rapidly together with concerns related to habitat fragmentation, on the one side, and spread of invasive species or disease vectors, on the other. Our methodological framework has been applied here to identify corridors for migrations, which are particularly vulnerable to fragmentation, but it can be generalized to any movement-based ecological processes. For example, it could predict feeding corridors in fragmented ranges, dispersal routes for invasive species, or it could be used in a scenario framework to identify the most robust corridors to changes in climate or land use. Because our approach allows predict corridor-barrier *continua* with increased realism and higher spatiotemporal detail compared to available approaches, it has the potential to support the identification of a wide range of management options for species conservation and for the mitigation of human–wildlife conflicts. On a more theoretical perspective, it opens for the possibility to test for a wide range of hypotheses related to optimal *vs.* random movement behaviour in different ecological settings.

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## Data accessibility

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.4v13r> (Panzacchi *et al.* 2015).

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## Supporting Information

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

**Appendix S1.** The randomized shortest path model in a nutshell.

**Appendix S2.** Predicting the continuum between corridors and barriers to animal movements using Step Selection Functions and Randomized Shortest Paths.