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

'You shall not pass!': quantifying barrier permeability and proximity avoidance by animals

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Summary

1. Impediments to animal movement are ubiquitous and vary widely in both scale and permeability. It is essential to understand how impediments alter ecological dynamics via their influence on animal behavioural strategies governing space use and, for anthropogenic features such as roads and fences, how to mitigate these effects to effectively manage species and landscapes.

2. Here, we focused primarily on barriers to movement, which we define as features that cannot be circumnavigated but may be crossed. Responses to barriers will be influenced by the movement capabilities of the animal, its proximity to the barriers, and habitat preference. We developed a mechanistic modelling framework for simultaneously quantifying the permeability and proximity effects of barriers on habitat preference and movement.

3. We used simulations based on our model to demonstrate how parameters on movement, habitat preference and barrier permeability can be estimated statistically. We then applied the model to a case study of road effects on wild mountain reindeer summer movements.

4. This framework provided unbiased and precise parameter estimates across a range of strengths of preferences and barrier permeabilities. The quality of permeability estimates, however, was correlated with the number of times the barrier is crossed and the number of locations in proximity to barriers. In the case study we found that reindeer avoided areas near roads and that roads are semi-permeable barriers to movement. There was strong avoidance of roads extending up to *c*. 1 km for four of five animals, and having to cross roads reduced the probability of movement by 68·6% (range 3·5–99·5%).

5. Human infrastructure has embedded within it the idea of networks: nodes connected by linear features such as roads, rail tracks, pipelines, fences and cables, many of which divide the landscape and limit animal movement. The unintended but potentially profound consequences of infrastructure on animals remain poorly understood. The rigorous framework for simultaneously quantifying movement, habitat preference and barrier permeability developed here begins to address this knowledge gap.

Key-words: animal movement, connectivity, fences, movement ecology, *Rangifer tarandus*, reindeer, resistance, resource selection, roads, step selection

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Introduction

Understanding how the biotic and abiotic environment affects the movement and distribution of organisms is a central objective of movement ecology. One aspect of this research is quantifying the degree to which the environment impedes or facilitates movement (Fahrig 2007; Spear *et al.* 2010) and the consequences of this for animal space use. Movement is a key strategy employed by animals to mediate trade-offs in life-history requirements arising from heterogeneous habitat distribution. Impediments to movement, therefore, have the potential to adversely affect the ability of organisms to fulfil those requirements. While much work has been done on modelling habitat preference and movement (though usually not both simultaneously), understanding the effects of impediments to movement has received relatively little attention. Recent work has begun to quantify the influence of impediments on migrations at landscape scales (Singh *et al.* 2012; Panzacchi, Van Moorter & Strand 2013a; Sawyer *et al.* 2013; Panzacchi *et al.* this issue), proximity avoidance effects of roads on population distribution (Fortin *et al.* 2013; Leblond, Dussault & Ouellet 2013) and functional responses in road crossing behaviour (Beyer *et al.* 2013).

All movement incurs a cost to the individual in terms of energy, time (opportunity cost) and exposure to risk (Ricketts 2001; Rothermel & Semlitsch 2002; Baker & Rao 2004; Fahrig 2007). For example, the cost of movement to an ungulate moving through dense forest may be influenced by tree and snag density (reducing movement rate and increasing the energy cost of movement), limited availability of forage (opportunity cost relative to open habitats) and possibly an increased risk of predation arising from reduced ability to detect or evade predators (mortality risk). We define a movement impediment as any feature of the environment that increases the cost of movement. Because movement is not instantaneous, all geographic space has some positive movement cost, though this cost can approach zero for organisms that incur trivial energy and opportunity costs and little exposure to risk.

Impediments to movement can take many forms and have a variety of effects on movement and distribution. Here, we use 'impediment' as an umbrella term that includes four more specific categories of impediments to movement: barriers, obstacles, impedances and constraints. The distinction between these categories is based on whether they can be crossed and/or circumnavigated (or neither). We define 'barriers' as features that can be crossed but not circumnavigated. Hence, an animal must cross a barrier in order to reach some part of space, and the degree to which a barrier inhibits such movement is its 'permeability'. 'Obstacles' can be circumnavigated but not crossed (they have impermeable boundaries) and thus increase the effective distance between two locations separated by an obstacle (i.e. the distance that must be travelled to circumnavigate the obstacle, which is at least as great as the straight-line distance between those locations). 'Impedances' can be crossed or circumnavigated, implying the animal must evaluate the trade-off between the costs of crossing the impedance (the barrier effect) vs. the costs of circumnavigation (the obstacle effect). Finally, 'constraints' can neither be crossed nor circumnavigated and therefore impose absolute limits on distribution. A research programme aiming at a mechanistic understanding of movement requires comparative quantification of the behavioural strategies employed by animals in response to each of these four types of impediments on movement and distribution. Here, we contribute to this endeavour by exploring the effect of the first category: barriers.

We present a framework for quantifying the response of animals to barriers, including proximity effects and crossing effects, in the context of movement and habitat preference. Proximity effects occur when the probability of space use is modified as a function of distance to the barrier. For example, a barrier may decrease or increase the density of use around it, thereby increasing or decreasing the density of used locations further away if animals avoid it (Fortin *et al.* 2013) or congregate against it (Loarie *et al.* 2009). Crossing effects reflect the permeability of the barrier and have previously been quantified by comparing the crossing distributions of animal movement paths to simulated movement paths (Shepard *et al.* 2008; Beyer *et al.* 2013), though this approach does not account for proximity or other habitat selection effects. The major challenge is to separate the response to barriers from the confounding effects of habitat preference and intrinsic movement capacity. Here, we propose a framework to do exactly that while simultaneously quantifying both proximity and permeability effects of potential barriers.

As a proof of concept, we focus on linear, physical barriers that are fixed in space but may have variable permeability in time, though this framework can be extended to other types of barriers. We used simulations to illustrate our estimation framework and applied this method to quantify the barrier effects of roads for wild mountain reindeer (*Rangifer tarandus tarandus*) in Norway. Barriers that arise from anthropogenic development and land management (e.g. roads, fences) are of particular conservation concern because of their abundance and ubiquity in many landscapes. In our case study, we found that the permeability of roads to reindeer was low and that areas in close proximity to roads were often avoided. We discuss the ecological implications of these barrier effects on foraging efficiency and predator–prey dynamics.

Materials and methods

MODELLING EFFECTS OF IMPEDANCES ON MOVEMENT

Our starting point is the framework of Rhodes *et al.* (2005) and Forester, Im & Rathouz (2009) that defines the probability of an animal moving from location a to location b (a 'step') in a given time interval and conditional on habitat covariates, X, at location b to be:

$$f(b|a,X) = \frac{\phi(a,b,\Delta t;\theta)\omega(X_b;\beta)}{\int_{c\in D}\phi(a,c,\Delta t;\theta)\omega(X_c;\beta)dc} \quad \text{eqn 1}$$

where $\phi(a,b,\Delta t;\theta)$ is defined as an habitat-independent movement kernel (HIMK, sometimes referred to as the resource-independent movement kernel) describing how the animal would move over time interval Δt in the absence of habitat influences, and $\omega(X;\beta)$ is the resource selection function (RSF) describing the use of habitat X relative to its availability and conditional on the availability of all habitats to the animal (Aarts *et al*. 2008; Matthiopoulos *et al*. 2011). 'Use' refers to habitat that has been encountered and selected, while 'availability' defines the habitat that could potentially be encountered by the animal (Lele *et al*. 2013). The shape of the HIMK is determined by parameter vector θ, while parameter vector β represents the habitat preferences. The numerator is normalized by the denominator, integrated over all locations, c, within the spatial domain, D. This model can be extended to higher orders by including the locations of the animal at previous steps (see Forester, Im & Rathouz 2009) and incorporating directional persistence of sequential steps.

Habitat is conceptualized as a point in multidimensional environmental space (Aarts *et al*. 2008; Hirzel & Lay 2008), each dimension representing a biotic or abiotic environmental variable related directly (e.g. forage biomass and quality) or indirectly (e.g. elevation) to the use of a location by the animal (Beyer *et al*. 2010). Environmental variables can be static or dynamic in time (e.g. slope and predator density, respectively) and may be positively or negatively associated with use. The movement path can be characterized as a series of points (a, b) or lines ($a\rightarrow b$). In the former case, the matrix of habitat covariates, X, is based on the habitat at point locations b and c (for X_b and X_c, respectively). In the latter case, X is based on the habitat characteristics along each line ($a\rightarrow b$ for X_b and $a\rightarrow c \in D$ for X_c). Both designs can be implemented within the framework presented here.

Functional responses in preference describe the change in preference for a habitat as a function of the availability of all other habitats (Mysterud & Ims 1998; Aarts *et al*. 2008) and can be estimated by writing the β coefficients of the RSF as functions of the availability of all environmental units (Matthiopoulos *et al*. 2011). Under the assumption that the time between consecutive steps is long enough to ensure that the animal experiences a representative sample of the entire landscape, the RSF can be approximated as a loglinear function $\omega(X_b;\beta) = e^{X_b\beta}$.

Here, we wish to quantify two principal effects of barriers on movement. First, the permeability of the barrier (κ) is a measure of the degree to which the barrier allows an animal to move between two locations across the barrier. Secondly, barriers may influence space use in proximity to the barriers, which relates to habitat preference. Hence, we define the probability of an animal moving from location a to location b in a given time interval and conditional on barrier permeability κ and habitat covariates, X, at location b to be:

$$g(b|a,X) = \frac{\phi(a,b,\Delta t;\theta)\omega(X_b;\beta)\psi(a,b;\kappa)}{\int_{c\in D}\phi(a,c,\Delta t;\theta)\omega(X_c;\beta)\psi(a,c;\kappa)dc} \quad \text{eqn 2}$$

where $\psi(a,b;\kappa)$ is 1 when there is no barrier between locations a and b, and κ otherwise. Thus, κ represents the permeability of the barrier in the range [0,1], where 0 is an impermeable barrier and 1 represents no barrier effect. The effect of proximity to impedances on habitat preference is modelled by adding a covariate to X indicating the distance to the nearest barrier.

In the simplest case, κ is a constant that applies to all barriers. Alternatively, κ could be implemented to reflect heterogeneity in permeability. For example, κ could be indexed (κ_i) to estimate permeabilities for different barrier types or discrete behavioural states or could be incorporated into a continuous expression that estimated how κ changes as a function of time of day or barrier width. There is great flexibility in how κ can be implemented in this framework, which facilitates the evaluation of competing models of barrier permeability.

The integral in the denominator of eqn 2 can make fitting this model to data difficult. Following Rhodes *et al*. (2005), a discrete space approximation of the integral can be used instead, provided that the interval of discretization is sufficiently small:

$$g\prime(b|a,X) = \frac{\phi(a,b,\Delta t;\theta)\omega(X_b;\beta)\psi(a,b;\kappa)}{A\sum_{c=1}^{N}\phi(a,c,\Delta t;\theta)\omega(X_c;\beta)\psi(a,c;\kappa)} \quad \text{eqn 3}$$

where N is the number of cells in discretized space D, and A is the area of each of these cells (or length in the case of a 1D application). The spatial domain D represents all geographic space, though in practice this domain must be constrained to satisfy computational limitations.

SIMULATION STUDY

As a proof of concept, we simulated the movement of an animal in continuous 1D space characterized by habitat heterogeneity and the presence of a semi-permeable barrier to movement at location $x = 0$, and then attempted to recover parameter values using maximum likelihood estimation. Space was wrapped at the boundaries $x = -5$ and $x = 5$ (i.e. the spatial domain was the circumference of a circle), and the habitat variable was defined by the function $H(x) = \cos(2\pi x/5 + 1)$ (Fig. 1), such that the habitat varied smoothly over the entire landscape at a scale larger than the movement step. The distance units are arbitrary, and the spatial dimension (the range of x-values) is only important in the context of the dispersion of the movement kernel.

The simulation algorithm involved sampling 2000 proposal steps from the HIMK. For each proposal step, the habitat value was determined from $H(x)$, and steps crossing the barrier were identified. The likelihood of taking each step was determined from $g'(b|a,X)$ (eqn 3) whereby the denominator was calculated by discretizing space into $N = 10\,000$ units of length $A = 10^{-3}$. A single 'accepted' step was sampled from the set of proposal steps in proportion to the magnitude of the likelihood. This process was repeated, sampling new proposal steps each time, until the target path length was achieved. Simulations were implemented in R (Appendix S1, Supporting information; R Development Core Team 2012). Note that because the movement kernel was small relative to the domain of space, it was not possible for a step to cross both the limits of space (-5 to 5) and the barrier, which simplifies the simulation algorithm.

To estimate parameters from the simulation, the log-likelihood function $g'(b|a,X)$ (eqn 3) was maximized with respect to the movement, preference and permeability parameters (θ,β and κ, respectively) using the Nelder-Mead algorithm (Nelder & Mead,

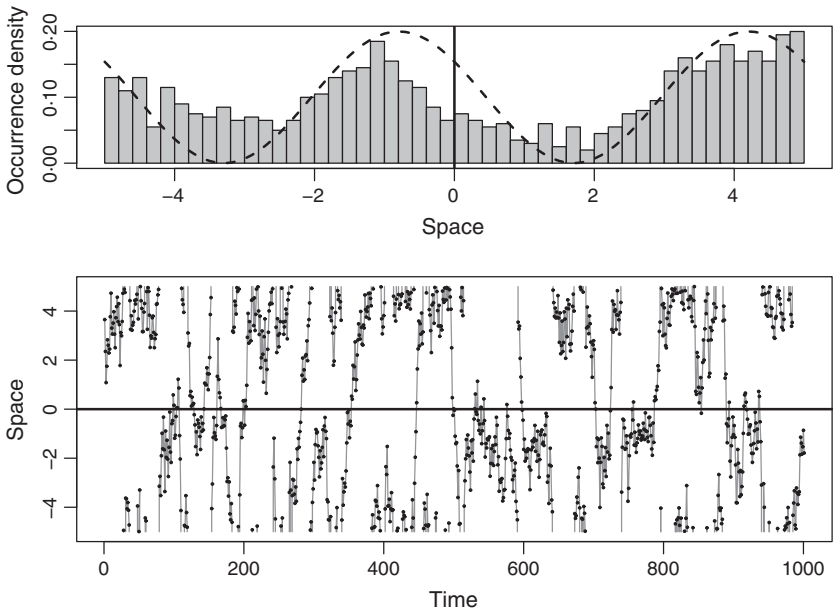

Fig. 1. Representative example of movement path simulation. (top) Density of movement locations (grey bars) in 1D space (x axis, wrapped at boundaries) given selection for habitat (dashed line) and a semi-permeable barrier to movement (black line at $x = 0$, 40% permeable). (bottom) The progression of movement path locations through time (x axis) and in relation to the semi-permeable barrier (line at $y = 0$). Note the spatial dimension is wrapped at the boundaries 5 and −5; thus, moves exceeding these boundaries appear at the opposite boundary.

1965) implemented with the 'optim' function in R (R Core Development Team 2012; Appendix S1, Supplementary Information)). Transformations were used to enforce appropriate limits on parameters, and parameters were back-transformed after fitting. An exponential transformation was used to enforce a lower limit of 0 on θ, and the inverse logit transformation $\exp(x)/(1 + \exp(x))$ was used to enforce limits of [0, 1] on κ. Confidence intervals for these parameter estimates were calculated from the Hessian matrix (±1·96 times the square roots of the diagonal elements of the covariance matrix). A parameter was considered to have been recovered if it fell within the 95% confidence interval. Paths of 1000 steps were simulated using a movement kernel characterized by a normal distribution with mean of 0 and standard deviation 1, starting at a random location [$U(-5, 5)$]. To assess whether parameter recovery varied in parameter space (β, κ), 10 replicates of movement paths were simulated at every pairwise combination of β = 0·0, 0·5, 1, 1·5, 2·0 and κ = 0·0, 0·25, 0·5, 0·75, 1·0, for a total of 250 simulated paths.

To investigate the drivers of bias (the difference between the parameter estimate and the true value) and confidence interval width for κ, we simulated a further 100 movement paths at fixed parameter values (θ = 1, β = 1·5, κ = 0·5). For each of these simulations, we recorded the number of times the barrier was crossed and the number of movement locations in close proximity to the barrier (within 0·673 distance units of the barrier, which is the distance defined by the 50% quantile of the movement kernel). Linear regression was used to quantify the relationship between bias or confidence interval width with barrier crossing frequency or the number of locations in proximity to the barrier (four regressions). The Akaike information criterion (AIC) was used to evaluate whether a linear ($y \sim x$) or quadratic ($y \sim x + x^2$) form was a better fit (defined as ΔAIC > 4).

CASE STUDY: REINDEER AND ROADS

GPS data for wild reindeer were collected within a larger project in Rondane South and Rondane North wild reindeer management areas, a mountainous region of central southern Norway (10° 46′ E, 61° 38′ N). As a case study, we used locations collected from five adult female reindeer (Fig. 2) every 3 h between 1 June to 29 September 2012 (N = 973, 960, 871, 971 and 974 locations, respectively) (Beyer 2014). Reindeer were immobilized from a helicopter and handled as described in Evans *et al.* (2013). Around 60% of the area is located above tree line between 1000 and 1500 m and is dominated by rocks and lichen heath; lower elevations (above 500 m) are characterized by a mix of meadows, grass and willow communities, as described in Nellemann *et al.* (2010). The area occupied by the reindeer used in this study extends between *c.* 400 and 1900 m and is fragmented by public and private roads (access to the latter is often restricted, so is characterized by lower traffic volumes than the former).

We simultaneously estimated the habitat-independent movement kernel, habitat preference and the permeability of roads as potential barriers by fitting $g'(b|a,X)$ (eqn 3) to the observed location data. Habitat covariates included elevation (km; ELEV) and distance to roads (km; DRD), both of which were raster format data sets with a spatial resolution of 100 m × 100 m. Elevation was evaluated because it is often correlated with other dimensions of habitat that are difficult to quantify but are important for habitat selection, such as forage quality or abundance, anthropogenic disturbance and weather variables. Distance to roads was evaluated because previous studies found that reindeer avoid regions in close proximity to roads (Panzacchi *et al.* 2013b). Our goal here, however, was not to evaluate competing models of habitat preference, but to demonstrate the utility of our approach for quantifying barrier permeability. We excluded from our analysis the crossing of short 'dead-end' road segments (Fig. 2), which are often narrower and have lower traffic densities than the rest of the road network. Furthermore, our framework is targeted specifically at barriers: roads that must be crossed when moving between consecutive locations. According to our definitions, dead-end road segments are impedances as they can be crossed or circumnavigated and therefore require a different modelling framework.

We evaluated two distributions describing the HIMK and used the Bayesian information criterion (BIC) to identify the model with greatest support. First, the HIMK was implemented as an unbiased bivariate normal distribution with equal variance in the x and y dimensions and no covariance, hence a

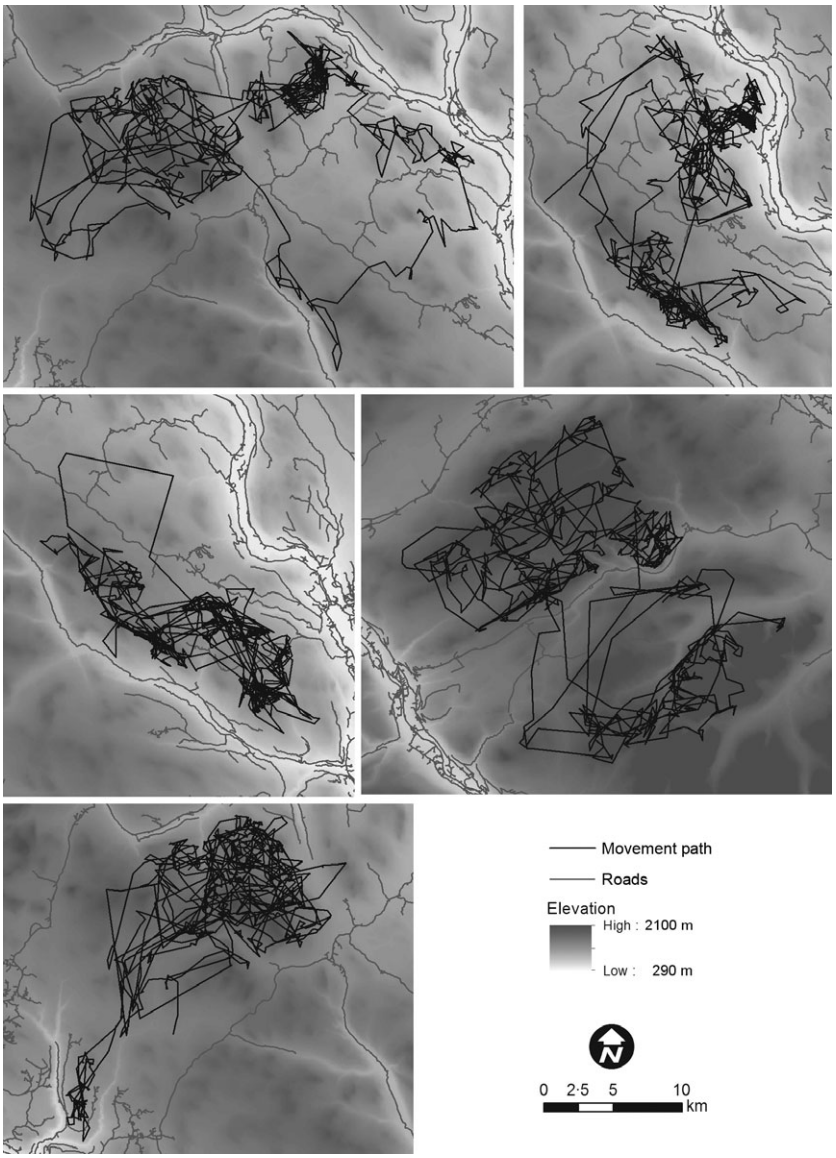

Fig. 2. Animal movement paths (black lines) derived from GPS telemetry locations of five adult female reindeer (panels) over one summer in two nearby areas (Rondane-South and Rondane-North) in central Norway. Reindeer must sometimes cross roads (grey lines) when moving around their range.

one-parameter distribution as the mean is always 0, that is $\psi(a,b;\theta) = \exp(-r^2/2\theta^2)/(2\pi r\theta\sqrt{2\pi})$, where r is the Euclidean distance between locations a and b. Secondly, the HIMK was implemented as an exponential distribution with mean $1/\theta$, that is $\psi(a,b;\theta) = \theta \exp(-\theta r)/2\pi r$. Other distributions could be used to model step lengths (e.g. Weibull or gamma distributions). The habitat preference function was modelled as $\omega(X;\beta) = \exp(\beta_1 \text{ELEV} + \beta_2 \text{ELEV}^2 + \beta_3 \text{DRD} + \beta_4 \text{DRD}^2)$. The response to barriers was implemented as a function that returned the estimated parameter κ if moving from $a \rightarrow b$ necessitated crossing a road, and 1 otherwise. The model was fit using the 'optim' function in R (R Development Core Team 2012), though Markov chain Monte Carlo methods could also be used.

Limits must be imposed on the spatial domain (D) for the problem to be computationally tractable. Spatial limits must be selected so that the estimation of the HIMK is not constrained (i.e. that the probability density of the HIMK is near 0 at the edges of these spatial limits). We defined D as all geographic space within a rectangle with edges 5 km from any reindeer location and determined whether this is reasonable using the fitted HIMK distribution (if the 99·9% quantile of the fitted HIMK was >5 km we would have extended the spatial domain and refit the models).

Results

SIMULATIONS

Estimated parameter values from simulations were generally accurate (Fig. 3) and displayed correct inference, that is expected recovery rates given the 95% confidence interval threshold used. The mean absolute difference between the maximum likelihood estimate and the true values of θ,β and κ was 0·005, 0·006 and 0·071, respectively, indicating accurate estimation. The 95% confidence intervals (CI) captured the true value of θ, β and κ in 239, 239 and 239 of 250 simulations, respectively. Only a single simulation failed on more than one-parameter estimation.

Of the 11 simulations that failed to estimate θ, the upper or lower confidence interval was very close to including the true estimate (all within 0·03), and there

were similar numbers of over- and underestimates (5 and 6, respectively). Parameter recovery success was not strongly related to parameter magnitude for β (1, 6, 1, 2 and 1 simulations failed to capture values of β of 0, 0·5, 1, 1·5 and 2, respectively) or κ (0, 2, 2, 2 and 5 simulations failed to capture values of κ of 0·0, 0·25, 0·5, 0·75 and 1·0, respectively). All simulations that failed to recover κ were underestimates, though all but one of these CIs were within 0·05 of the true estimate. The worst performing simulation underestimated by 0·244.

The realized distribution of step lengths decreased as a function of β (Fig. 4; linear regression, $y \sim \beta_0 + \beta_1 x$, $\beta_0 = 0{\cdot}99 \pm 3{\cdot}3 \times 10^{-3}$ SE, $\beta_1 = -0{\cdot}15 \pm 2{\cdot}7 \times 10^{-3}$ SE) but was unrelated to κ (linear regression, $y \sim \beta_0 + \beta_1 x$, $\beta_0 = 0{\cdot}84 \pm 0{\cdot}012$ SE, $\beta_1 = -0{\cdot}7 \times 10^{-3} \pm 0{\cdot}020$ SE). For example, the mean observed step length among all simulations in the absence of preference ($\beta = 0$) was 0·78 units, but dropped to 0·53 units when $\beta = 2$. This trend did not impact the estimation of θ (Fig. 3).

Overall, there was little evidence of bias in the maximum likelihood estimates, and most confidence intervals contained the true parameter value. Estimates for κ, however, appeared to be quite variable, especially at higher values of β and κ (Fig. 3). Bias in the estimate of κ was positively correlated with the number of times the movement path crossed the barrier (Fig. 5a; linear regression, $y \sim \beta_0 + \beta_1 x$, $\beta_0 = -0{\cdot}24 \pm 0{\cdot}063$ SE, $\beta_1 = 2{\cdot}1 \times 10^{-3} \pm 5{\cdot}1 \times 10^{-4}$ SE), but uncorrelated with the number of locations in proximity to the barrier (Fig. 5b; linear regression, $y \sim \beta_0 + \beta_1 x$, $\beta_0 = 1{\cdot}3 \times 10^{-2} \pm 2{\cdot}8 \times 10^{-2}$ SE, $\beta_1 = 3{\cdot}8 \times 10^{-5} \pm 1{\cdot}5 \times 10^{-4}$ SE). The width of the confidence intervals for the estimate of κ was positively associated with the number of barrier crossings (Fig. 5c; linear regression, $y \sim \beta_0 + \beta_1 x + \beta_2 x^2$, $\beta_0 = 0{\cdot}58 \pm 0{\cdot}21$ SE, $\beta_1 = -7{\cdot}0 \times 10^{-3} \pm 3{\cdot}5 \times 10^{-3}$ SE, $\beta_2 = 4{\cdot}3 \times 10^{-5} \pm 1{\cdot}4 \times 10^{-5}$ SE) and negatively associated with the number of locations in proximity to the barrier (Fig. 5d; linear regression, $y \sim \beta_0 + \beta_1 x + \beta_2 x^2$, $\beta_0 = 0{\cdot}69 \pm 0{\cdot}036$ SE, $\beta_1 = -2{\cdot}5 \times 10^{-3} \pm 4{\cdot}1 \times 10^{-4}$ SE, $\beta_2 = 4{\cdot}2 \times 10^{-6} \pm 1{\cdot}1 \times 10^{-6}$ SE).

REINDEER

The exponential distribution performed better than the normal distribution as a description of the HIMK (for 3 h interval movements) for 4 of the 5 reindeer (the difference in BIC between the normal and exponential distribution models was −207, 191, 125, 365 and 170, respectively). The estimated and observed mean step distances of the five reindeer were 0·72, 0·82, 0·96, 0·79, 1·08 km and 0·84, 0·75, 0·93, 0·74, 0·99 km, respectively (Table 1; Fig. 6). In all cases, the density of the HIMK is close to 0 at a distance of 3 km (Fig. 6), indicating that the 5 km margin around the extent of the reindeer locations is adequate to describe the spatial domain as any locations further than 3 km contribute little to the denominator of eqn 3.

There was evidence of habitat preference for elevation for two reindeer (Fig. 6n,r) that favoured higher elevations. In contrast, there was strong preference with respect to distance to the nearest road for four of the five reindeer (Fig. 6c,g,k,o). These four reindeer were less likely to select steps ending near roads (*c*. 0–1 km). There was also some evidence that the reindeer were less likely to select

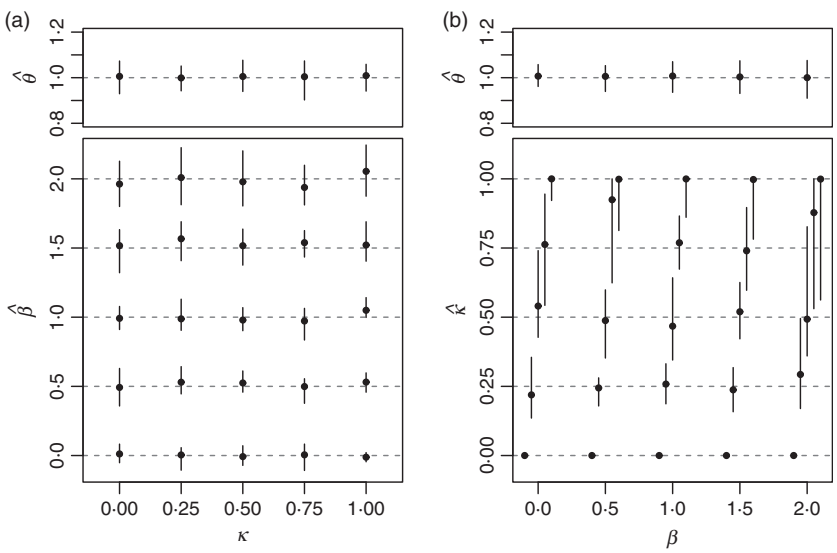

Fig. 3. Summary of fitting a movement model to simulated movement paths to assess parameter recovery and potential bias. Sets of 10 paths were simulated at every combination of five levels of habitat selection (β) and five levels of barrier permeability (κ), with constant movement kernel θ. In both plots, dots represent the mean parameter estimate among each set of 10 simulations, and the lines are the 95% confidence intervals of those parameter estimates. Dashed horizontal lines indicate the true parameter values. There was no evidence of bias in the estimation of θ and β across all levels of κ (a). Similarly, there was no evidence of bias in the estimation of θ and κ across all levels of β (b), though there was considerable range in estimate of κ. Note a small *x*-axis offset has been applied in (b) to prevent overlap of quantile lines.

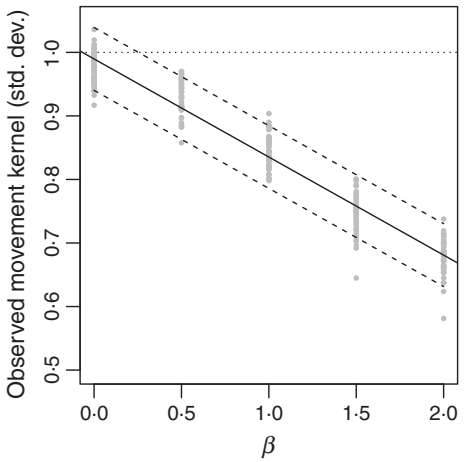

Fig. 4. Change in the observed movement kernel (specifically, the standard deviation describing a normal distribution; *y* axis) as a function of strength of selection (β) based on 250 simulated movement paths (points) of length 1000 steps. For all simulations, the habitat-independent movement kernel (HIMK) is a normal distribution with standard deviation 1·0. As the strength of selection increases, movements become increasingly limited by the effect of habitat selection. When selection is strongest, there is considerable discrepancy between the observed (empirical) kernel and the underlying HIMK.

steps far away (>5 km) from roads (Fig. 6c,g,k,o). The road permeability estimates ranged from 0·01 to 0·96 (Table 1; Fig. 6), though the confidence intervals for two of these estimates were wide (Fig. 6l,p). The frequency of observed road crossings for each of the reindeer was 4, 17, 0, 6 and 5 crossings. The avoidance of areas near roads may contribute to the uncertainty in the estimate of permeability.

Discussion

Having defined barriers as impedances to movement that cannot be circumnavigated, but must be crossed to move between two regions, we establish a framework for quantifying barrier effects in the context of movement and habitat preference. We demonstrated that parameters defining movement, preference and barrier permeability can be reliably recovered from simulated paths. In cases where parameter recovery was not successful, the estimate was not consistently biased, indicating inferences based on such an analysis would likely be robust to parameter estimation error. Applying this framework to the movement of reindeer in Norway, we demonstrated that, after accounting for the intrinsic movement patterns and habitat preference, roads are effective barriers to movement. Movement between two areas separated by a road that cannot be circumnavigated was, on average, reduced by 68.6% (range 3.5–99.5%) relative to the expected movement rate in the absence of the road. Furthermore, four of five reindeer avoided areas close to roads (within *c*. 0–1 km; Fig. 6) relative to their availability in the landscape. By simultaneously quantifying both proximity avoidance and low barrier permeability, we show how roads reduce

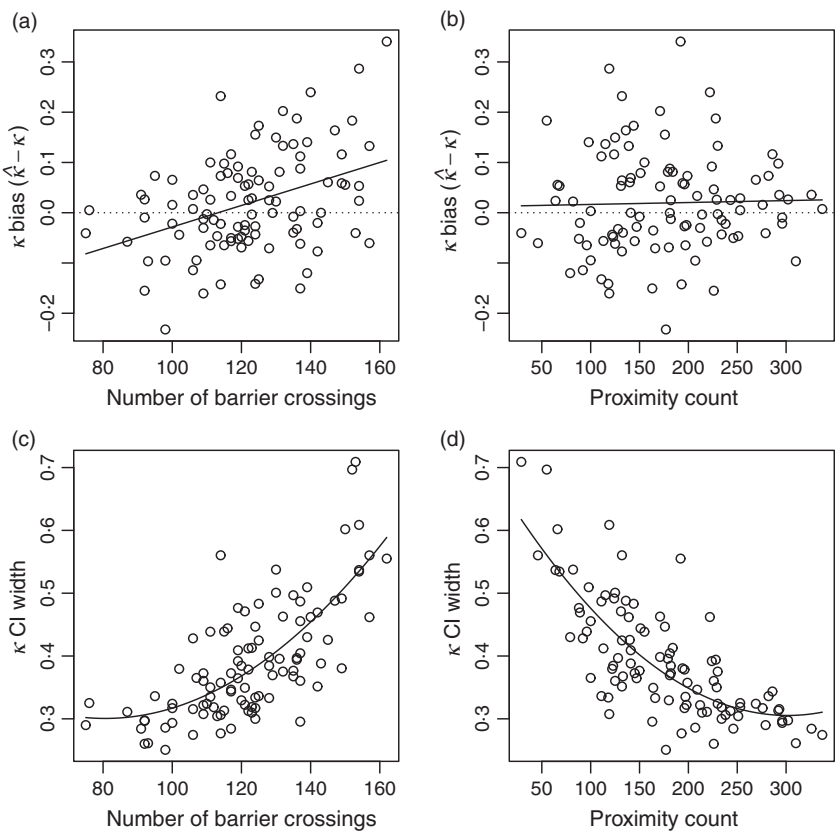

Fig. 5. Analysis of factors influencing bias (the difference between the estimate and true value) and confidence interval width for the permeability variable κ. Bias was positively correlated with the number of barrier crossings (a), but unrelated to the number of movement path locations in close proximity (a distance defined by the 50% quantile of the movement kernel) to the barrier (b). The width of the confidence interval for κ was positively correlated with the number of crossings (c) but negatively correlated with the number of locations close to the barrier (d).

Table 1. Maximum likelihood parameter estimates (and 95% confidence intervals) for each of the five individuals (id). The parameters represent the movement kernel parameter (σ, representing the standard deviation of a normal distribution for id 1, or the rate parameter of an exponential distribution for all other animals), the permeability of roads (κ) and habitat preference for elevation (quadratic, β_1 and β_2) and distance to roads (quadratic, β_3 and β_4)

id	σ	κ	β_1	β_2	β_3	β_4
1	0·90 (0·86, 0·95)	0·01 (0·00, 0·02)	3·38 (−1·50, 8·27)	−0·90 (−3·51, 1·71)	0·89 (0·64, 1·14)	−0·12 (−0·17, −0·08)
2	1·22 (1·14, 1·31)	0·33 (0·18, 0·51)	1·50 (−2·74, 5·73)	0·03 (−2·51, 2·58)	1·25 (0·82, 1·68)	−0·27 (−0·39, −0·15)
3	1·04 (0·97, 1·12)	0·05 (0·00, 0·91)	4·52 (−2·62, 11·66)	−1·59 (−4·86, 1·69)	0·65 (0·34, 0·96)	−0·09 (−0·13, −0·05)
4	1·27 (1·18, 1·36)	0·96 (0·00, 1·00)	9·32 (0·91, 17·73)	−3·76 (−8·24, 0·73)	1·17 (0·76, 1·58)	−0·27 (−0·40, −0·15)
5	0·93 (0·87, 0·99)	0·18 (0·07, 0·39)	9·26 (1·85, 16·68)	−2·72 (−5·39, −0·05)	0·00 (−0·24, 0·24)	0·01 (−0·02, 0·04)

the effective area of reindeer habitat by fragmenting the landscape into regions delineated by networks of roads that are infrequently crossed.

The inferred permeability and proximity effects of barriers may have important implications for foraging and fitness. We hypothesize that barrier effects could reduce foraging efficiency by reducing the effective area of habitat that is accessible by reindeer (the proximity avoidance effect) and by reducing interpatch movement (the permeability effect). Previous work has demonstrated that lichen biomass is higher near infrastructure and attributed this to the loss of feeding opportunity due to avoidance effects (Vistnes *et al.* 2004; Dahle, Reimers & Colman 2008). Avoidance of proximity to roads results in habitat loss and fragmentation and increases the effective distance between patches. The marginal value theorem (Charnov 1976) predicts that increasing transit times and decreasing connectivity among patches will result in animals staying longer in foraging patches, further depleting them but at a reduced rate of energy intake. Hence, compared with landscape without roads, optimal foraging theory would predict that foraging efficiency, and consequently, fitness is reduced in the landscape partitioned by roads. That said, semi-permeable barriers may constrain movement for a period of time, but ultimately animals may cross them and use habitat on the other side of the barrier extensively. The long-term average spatial distribution may, therefore, be similar to the distribution had barriers been absent even if, over shorter periods, barriers limit movement and distribution. The foraging consequences of roads must be evaluated therefore in the context of rates of interpatch movements and the density of barriers, which determines the degree of landscape fragmentation. Quantifying this mechanistic basis for understanding the effects of roads on fitness via their effects on foraging strategies is an important area for future work.

Another possible ecological consequence of barriers is making prey location more predictable to predators or hunters, and also more accessible if barriers facilitate predator movement (e.g. roads). Mitchell & Lima (2002) suggest that animals may move among patches more frequently than would be predicted by optimal foraging theory in order to reduce predation risk by being less predictable. Conversely, if barriers reduce interpatch movement, and animals consistently avoid being near roads such that their density increases some distance away from roads, then they are necessarily going to be more predictable in space (Dyer *et al.* 2002; Fortin *et al.* 2013). Furthermore, predators can use roads to more rapidly move around a landscape, further improving their ability to access prey (McKenzie *et al.* 2009). Although less obvious than some of the direct effects of roads on animals, such as mortality (Pickles 1942; Fahrig & Rytwinski 2009) and habitat loss (Forman & Alexander 1998; Saunders *et al.* 2002), changes to foraging efficiency and predator–prey dynamics could have profound longer-term effects on survival and reproduction (Basille *et al.* 2013).

From a management perspective, it is important to evaluate both barrier permeability and proximity effects. Permeability of barriers can be altered through the construction of over- or underpasses, tunnels, fences and corridors and management of roadside vegetation (Clevenger & Waltho 2000). There is little understanding, however, of how management could reduce the proximity effects of barriers, particularly as the cause of this avoidance is not understood and may be multifaceted (noise, visual cues, perceived threat, etc). For some species, it may be possible to partially mitigate proximity effects through barrier concealment (potentially visual and auditory effects) or other forms of landscape design. Further work in this regard is warranted, particularly as roads are pervasive in many landscapes (Forman & Alexander 1998) and fencing is increasingly being used to manage human–wildlife conflicts (Hayward *et al.* 2009) even though we do not fully understand the ramifications of establishing these barriers. It would be valuable for future work on reindeer to evaluate how permeability and avoidance are influenced by traffic volume to better define what aspects of roads the animals are responding to (e.g. see Leblond, Dussault & Ouellet 2013). Moving some portions of roads into tunnels may be one of the most effective options at reducing road effects on reindeer.

Our simulation work demonstrated that the realized (empirical) step length distribution arose from the interaction of the HIMK and habitat preference. Strong selection acted to constrain movement by placing greater relative weight on the RSF compared with the HIMK. Although this is not an issue related to barriers, it is an observation that has important implications for the estimation of habitat preference. Specifically, using the

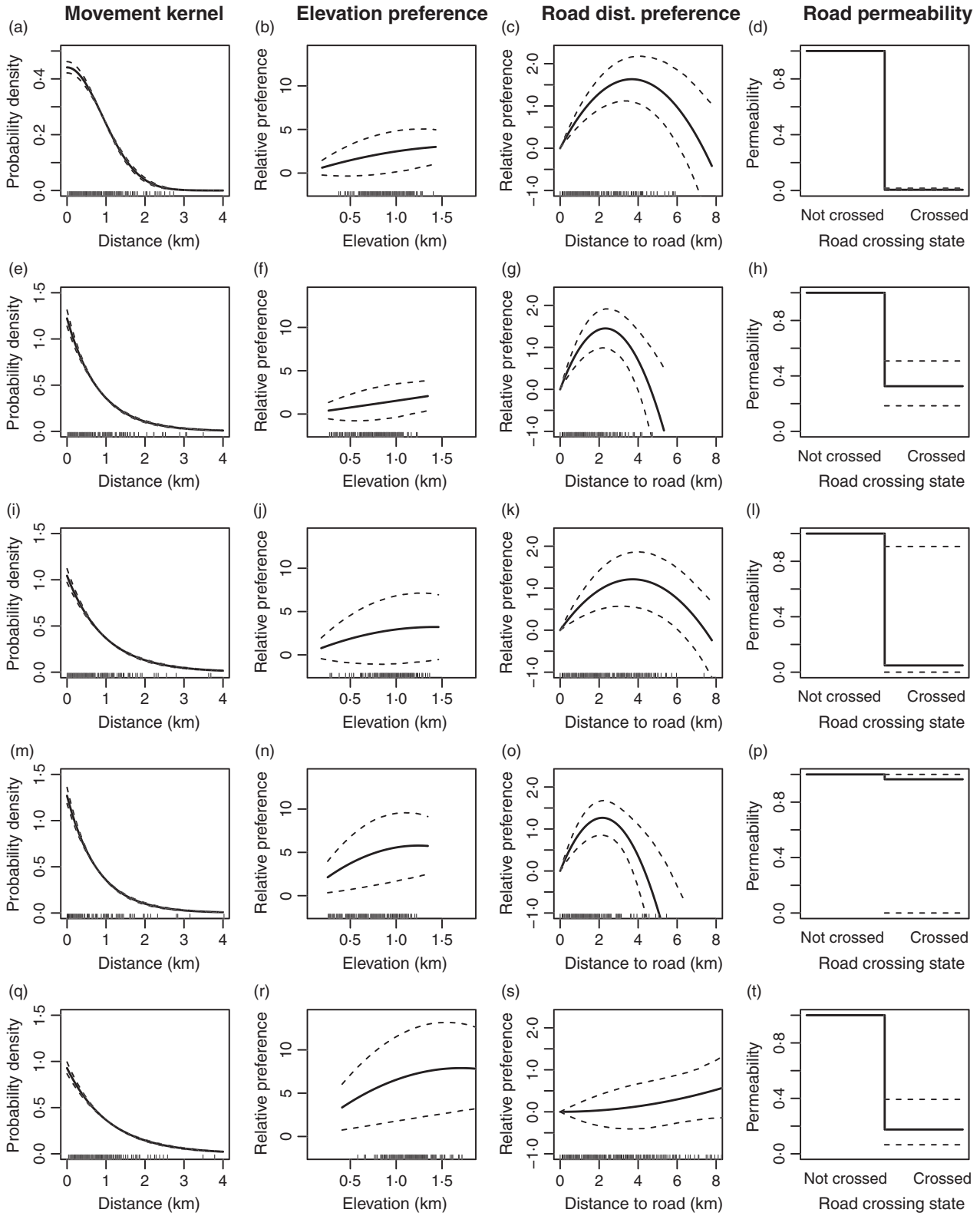

Fig. 6. For each of five reindeer (rows of plots), the mean estimates (solid lines) of the movement kernel (column 1), relative resource preferences for elevation (column 2) and distance to roads (column 3), and road permeability step function (column 4). The 95% CIs are shown as dashed lines, and the marks along the *x* axis (first three columns of plots) are a random sample from the distribution of available values.

observed (empirical) movement distribution to quantify availability (a 'step selection function' design; Fortin, Morales & Boyce 2005) may only be justified when selection is weak and could result in biased selection estimates (Forester, Im & Rathouz 2009; Lele *et al.* this issue). We show that estimating the HIMK and the

habitat preference models simultaneously (rather than making *a priori* assumptions about the HIMK) facilitates unbiased parameter estimation. Furthermore, this trade-off between strength of selection and the realized movement distribution could help explain variation in movement patterns among study areas or landscapes.

The simulation study also provides insight into some difficulties with quantifying permeability. Estimates of permeability are likely to be poor if the animal crosses a barrier rarely or too frequently or is often far from a barrier. Specifically, we found that bias in the estimate of permeability was positively correlated with the number of barrier crossings (Fig. 5a), while the width of the confidence intervals around the estimate was positively associated with the number of crossings and negatively associated with the number of locations in proximity to the barrier. Clearly, animal locations that are far from a barrier (relative to the movement ability of the animal) provide very little information about the permeability of that barrier. Fitting this model to data from several animals occurring across a range of barrier densities and proximities is likely to provide the strongest inference about permeability.

The framework presented here brings together recent advances in movement modelling including the development of mechanistic movement models (Rhodes *et al.* 2005; Moorcroft, Lewis & Crabtree 2006; Moorcroft & Barnett 2008) with approaches for estimating functional responses in habitat preference (Matthiopoulos *et al.* 2011) in order to quantify the effects of barriers on movement and habitat selection. Although often more challenging to fit compared to simpler statistical habitat selection models (such as generalized linear models), mechanistic movement models have the advantage of more robust parameter estimation and greater objectivity as they do not require subjective decisions regarding the domain of availability. Furthermore, their flexibility facilitates adapting them to address many types of movement modelling problems as we have demonstrated by using them to quantify barrier permeability and proximity avoidance. Thus, we strongly advocate the mechanistic movement model approach to address habitat preference and barrier problems.

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Data accessibility

The code for the simulation analysis is included in the Supporting Information. The data for the reindeer case study have been archived and are publicly accessible (Beyer 2014).

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Supporting Information

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

Appendix S1. The R code used to simulate movement paths and to fit the movement models to both the simulated and reindeer case study data sets.