Article:

Bastille-Rousseau, G., Murray, D.L., Schaefer, J.A. et al. (3 more authors) (2018) Spatial scales of habitat selection decisions: implications for telemetry-based movement modelling. Ecography, 41 (3). pp. 437-443. ISSN 0906-7590

https://doi.org/10.1111/ecog.02655

Title: Spatial scales of habitat selection decisions: implications for telemetry-based movement modelling

Guillaume Bastille-Rousseau[a,b,c*], Dennis L. Murray[c], James A. Schaefer[c], Mark A. Lewis[d], Shane Mahoney[e], Jonathan R. Potts[f].

[a] Department of Environmental and Forest Biology, State University of New York, College of Environmental Science and Forestry, Syracuse, New York, 13210, USA
[b] Roosevelt Wild Life Station, State University of New York, College of Environmental Science and Forestry, Syracuse, New York, 13210
[c] Environmental and Life Sciences Graduate Program, Trent University, Peterborough, Ontario, K9L 0G2, Canada
[d] Centre for Mathematical Biology, Department of Mathematical and Statistical Sciences and Department of Biological Sciences, University of Alberta, Edmonton, Alberta, T6G 2R3, Canada
[e] Conservation Visions Inc,, P.O. Box 5489 – Stn C, 354 Water St, St. John's, Newfoundland and Labrador, A1C 5W4, Canada
[f] School of Mathematics and Statistics, University of Sheffield, Sheffield, UK.

* Corresponding author: gbastill@esf.edu, (315) 751-8559

Abstract

Movement influences a myriad of ecological processes operating at multiple spatial and temporal scales. Yet our understanding of animal movement is limited by the resolution of data that can be obtained from individuals. Traditional approaches implicitly assume that movement decisions are made at the spatial and temporal scales of observation, although this scale is typically an artifact of data-gathering technology rather than biological realism. To address this limitation, we used telemetry-based movement data for caribou (*Rangifer tarandus*) in Newfoundland, Canada, and compared movement decisions estimated at the temporal resolution of GPS relocations (2 hours) to a novel model describing directional movement to areas reachable over an extended period. We showed that this newer model is a better predictor of movement decisions by caribou, with decisions made at the scale of ~2 km, including the strong avoidance of dense coniferous forest, an outcome not detectable at the scale of GPS relocations. These results illustrate the complexity of factors affecting animal movement decisions and the analytical challenges associated with their interpretation. Our novel modelling framework will help support increased accuracy in predictive models of animal space-use, and thereby aid in determining biologically meaningful scales for collecting movement and habitat data.

Key-words: global positioning system, movement modelling, Newfoundland caribou, random walk, resource selection analysis, step-selection function.

Introduction

Understanding organism movement is a fundamental challenge in ecology (Sutherland et al. 2013). The movements of animals influence ecological processes operating at multiple spatial and temporal scales (Nathan et al. 2008), with repercussions for individual fitness as well as population, community, and ecosystem function (Turchin 1998, Holyoak et al. 2008, Fortin et al. 2015). Nathan et al. (2008) proposed a unifying paradigm of an organism's movement derived from interactions with the environment, its internal state, and mechanical and navigational properties of the organism. Moreover, realistic modelling of animal movement often needs to be applied at biologically-relevant scales, sometimes multiple scales. This can represent a daunting task for ecologists, owing to the highly dynamic interactions of organisms with their environment and internal state. Mechanical-navigational properties alone may offer limited insight into the determinants of animal movement.

Lagrangian models are useful for generating multi-segment trajectories of animal movement, akin to information typically acquired from satellite telemetry (Smouse et al. 2010). Simpler expressions of these models, such as random walks, assume little navigation capacities, but focus extensively on the motion capacity of animals by fitting a specific step-length distribution (Turchin 1998). More complex expressions, such as correlated random walk or biased random walk models, integrate navigational capacities by adding persistence in movement or attraction to specific area, respectively (Farnsworth and Beecham 1999, Bergman et al. 2000). When combined with information about the landscape and resource distribution, random walk models can improve our understanding of resource selection and thereby generate more realistic patterns of space-use (Moorcroft and Lewis 2006, Smouse et al. 2010, Fortin et al. 2013, Potts et al. 2014, Bastille-Rousseau et al. 2015). Indeed, it seems that most movement behavior can be reproduced by a mixture of random walk models operating at different scales (Benhamou 2014). Therefore, by building on these developments, ecologists can focus more on understanding the factors driving navigational process, including elements related to orientation, memory, and the formulation of a cognitive map by an animal (Van Moorter et al. 2009, Avgar et al. 2013, Fagan et al. 2013, Merkle et al. 2014, Schlägel and Lewis 2014, Potts and Lewis 2016).

Despite these conceptual improvements, our understanding of animal movement is still often limited by the resolution of field data. Although rarely discussed, many approaches inherently assume that navigational processes and associated decisions are made at the spatial and temporal scale of the data (Fleming et al. 2014, Schlägel and Lewis 2016a, b). For example, the increasingly popular step selection function (SSF; Fortin et al. 2005, Forester et al. 2009, Avgar et al. 2016) integrates elements of resource selection by combining a correlated random walk with the local attraction to specific resources. Its estimation involves conditional comparison of an actual step (between two locations) with a series of random steps initiated from the same location that assess available habitat based on the motion-related capacity of the organism. In such a framework, inferences regarding movement decisions for a given resource are contingent upon behavioral processes operating at the movement step scale. Similar issues also prevail in the state-space modelling literature (Morales et al. 2005, Langrock et al. 2012)

Furthermore, navigational abilities may be driven by behavioral processes operating at different spatio-temporal scales (Fleming et al. 2014, Benhamou 2014). For instance, a migrating animal might orient its fine-scale movements toward habitat that provides foraging opportunities or low mortality risk, while ignoring habitat that has higher costs. Whereas these two processes – migration and interpatch movement – operate at distinct scales and can be represented independently (Benhamou 2014), an animal’s motivations related to migratory and interpatch movements likely compete in generating the observed distributions of step length, turning angle and habitat use, as captured by telemetry. Observations at the arbitrary scale of telemetry data could fail to capture decisions happening at either scale. The role of memory and cognition have been at the forefront of recent movement modelling (Van Moorter et al. 2009, Avgar et al. 2013, 2015, Fagan et al. 2013, Potts and Lewis 2016), but it remains unclear how differing spatio-temporal scales lead to variability in animal interactions with resources.

Here, we investigated the importance of decisions relative to environmental resources in animal movement and how its estimation can be influenced by the scale at which it is assessed. We focused on the motion and navigational capacities of Newfoundland caribou (*Rangifer tarandus* L.) during the calving period and tested how movement can be explained by a mixture of local or long-distance responses to specific resources. There are fourteen major caribou herds inhabiting the island of Newfoundland, with most female caribou exhibiting spring migration to traditional calving grounds. We compared an approach inspired by the specific SSF framework of Potts et al. (2014), that considers decisions at the scale of the GPS relocations, to a new model of long-distance decisions that capture movement in the direction of areas that an animal could reach over many hours or days. To examine the effect of movement on seasonal scale behavior, we compared resource use and selection of caribou to predicted patterns of use and selection based on the motion capacity of caribou. We hypothesized that selection toward certain resources and avoidance of others would be necessary in order to explain movement of caribou because the habitat selection of female caribou during post-calving represents a tradeoff for minimizing predation risk (at the broad scale) and foraging (at the fine scale). Accordingly, we predicted that caribou movement would be best represented by assessing resource selection at a longer distance than the one provided by GPS relocations (Bastille-Rousseau et al. 2015). We believe that the modelling framework proposed here will set the foundation for building predictive models of animal movement that are more reflective of realistic biological determinants, and thereby represent an improvement to traditional telemetry-based animal movement modeling.

Methods

Study area

Newfoundland is a 108,860-km² island at the eastern extremity of Canada (47°44N, 59°28W - 51°44N, 52°38W), with humid-continental climate and substantial year-round precipitation (Environment Canada 2013). Natural habitat consists mainly of coniferous and mixed forests of balsam fir (*Abies balsamea*), black spruce (*Picea mariana*), and white birch (*Betula papyrifera*) and, in some locations, substantial areas composed of bogs and heath or barren habitats. Our analyses were based on Landsat TM satellite imagery, with a resolution of 25 m, classified into 5 different habitat types: wetland habitats (Wetland), barren and other open habitats (Barren), mixed and coniferous open stand (CO), mixed and coniferous dense stand (CD), open water and other rarer habitats such as broadleaf stands, herbs and bryoids (Other) (Wulder et al. 2008). Anthropogenic disturbances were not extensive on these caribou ranges and consisted of logging, hydroelectric developments, and roads. We restricted our analysis to five important migratory herds located south of the main east-west highway that crossed the island.

Animal capture and monitoring

During 2006-2010, more than 200 caribou were captured, principally during winter, and fitted with global positioning system (GPS) collars that obtained locations every 2 hours. We focused on 140 adult females (361 caribou-years and 371,744 locations), 2006-2012, that resided in 6 herds. We limited our movement analysis to the crucial, post-migratory period of calving and post-calving (1 May - 1 August) when most caribou neonate mortalities occur (Bastille-Rousseau et al. 2016). All animal capture and handling procedures were consistent with the American Society of Mammologists guidelines (Sikes and Gannon 2011).

Statistical analyses

In Potts *et al.* (2014), a method was developed for inferring the probability of finding a caribou in a habitat $H(\boldsymbol{x})$, given that it was at position $\boldsymbol{y}$ in the previous step (2 hours previously) and arrived there on a trajectory θ_0. The model takes the form:

$$P_S(H(\boldsymbol{x})|\boldsymbol{y},\theta_0,W_S) = K_S(\boldsymbol{y},\theta_0)^{-1}\{A_S(H(\boldsymbol{x})|\boldsymbol{y},\theta_0)W_S[H(\boldsymbol{x}),H(\boldsymbol{y})]\} \qquad (1)$$

where $\boldsymbol{x}$ is the current position of the animal, $H(\boldsymbol{x})$ is the habitat type at $\boldsymbol{x}$, and $W_S[i,j]$ is the weight associated to moving from habitat j to habitat i. Here, i and $j \in \mathcal{H}$, the set of all possible habitat types. In equation (1), $A_S(j|\boldsymbol{y},\theta_0)$ represents the probability that an animal ends its step in habitat-type j, given that it starts at $\boldsymbol{y}$ and arrives there on trajectory θ_0, discounting the weighting due to habitat selection. This can be thought of as the 'availability' of habitat-type j, given $\boldsymbol{y}$ and θ_0. As in Potts *et al.* (2014), we found an approximate value for $A_S(j|\boldsymbol{y},\theta_0)$ by sampling 100 times from the distribution $\Phi(\mathbf{x}|\mathbf{y},\theta_0)$. Then $A_S(j|\boldsymbol{y},\theta_0)$ is defined to be the proportion of samples that land in habitat-type j. The function $K_S(\boldsymbol{y},\theta_0)$ ensures that $\int_\Omega P_S(H(\boldsymbol{x})|\boldsymbol{y},\theta_0,W_S)d\boldsymbol{x} = 1$, where Ω is the study area.

A drawback of this approach is that it assumes caribou make movement decisions on a 2-hour framework. In reality, since they have home ranges that are dozens of kilometers across, they are likely to make longer-scale decisions when moving. To test this hypothesis, we constructed a model describing probability of an animal moving towards a region of a given area (defined based on the proportion of each landcover within a circle of diameter D), at a distance R away from the animal, containing habitat of type i (see Figure 1). This model is:

$$P_L(i|\boldsymbol{y}, R, D, W_L) = K_L(\boldsymbol{y}, R, D)^{-1} A_L(i|\boldsymbol{y}, R, D) W_L[i, H(\boldsymbol{y})], \quad (2)$$

where W_L and A_L are the long-distance analogues of W_S and A_S respectively. More precisely, $W_L[i,j]$ is the weighting associated with moving from habitat-type j in the direction of the region of diameter D, at a distance R away from the animal, containing habitat of type i. $A_L(i|\boldsymbol{y}, R, D)$ denotes the proportion of habitat i in the circle, $S_{R,y}$ of radius R, centered at $\boldsymbol{y}$, after averaging each point over the smaller circle $C_{\theta,y,R,D}$, centred at a position of distance D away from $\boldsymbol{y}$ in direction θ. The function $K_L(\boldsymbol{y}, R, D)$ ensures that $\sum_{i \in \mathcal{H}} P_L(i|\boldsymbol{y}, R, D, W_L) = 1$. This situation is illustrated in Figure 1. Note that the circle $C_{\theta,y,R,D}$ may not be used by the animal, but might still provide information regarding movement decisions made by animals. Our goal is to evaluate, relative to all potential combinations of resources that are available to the animal over a specific distance, if the animal is more likely to direct its movement more (or less) frequently towards specific combination of resources.

Usually, the circle $C_{\theta,y,R,D}$ will contain more than one habitat, so it is necessary to generalize equation (2) by constructing the probability of moving from $\boldsymbol{y}$ towards a circle containing habitat types in the same proportions as those inside $C_{\theta,y,R,D}$. With this in mind, we let $H_L(\theta) = \{Q(i|\theta, \boldsymbol{y}, R, D)\}_{i \in \mathcal{H}}$ denote the set of proportions of habitat types $i \in \mathcal{H}$ found in the circle $C_{\boldsymbol{\theta},R,D}$. Here, $Q(i|\theta, \boldsymbol{y}, R, D)$ is the proportion of habitat i found in the circle $C_{\theta,y,R,D}$. Then we define:

$$P_L(H_L(\theta)|\boldsymbol{y}, R, D, W_L) = K_L(\boldsymbol{y}, R, D)^{-1} \sum_{i \in \mathcal{H}} A_L(i|\boldsymbol{y}, R, D) Q(i|\theta, \boldsymbol{y}, R, D) W_L[i, H(\boldsymbol{y})]. \quad (3)$$

We call Equation (3) the *long-distance model*, while Equation (1) is called the *local model*.

Given a set of consecutive locations $\boldsymbol{x}_0, \boldsymbol{x}_1, \ldots, \boldsymbol{x}_N$, we parameterize the models in equations (1) and (3) by maximizing the following likelihood functions, respectively:

$$L_S(\boldsymbol{x}_0, \boldsymbol{x}_1, \ldots, \boldsymbol{x}_N | W_S,) = \prod_{n=1}^{N} P_S(H(\boldsymbol{x}_n) | \boldsymbol{x}_{n-1}, \theta_{n-1}, W_S), \quad (4)$$

$$L_L(\boldsymbol{x}_0, \boldsymbol{x}_1, \ldots, \boldsymbol{x}_N | W_L,) = \prod_{n=1}^{N} P_L(H_L(\theta_n) | \boldsymbol{x}_{n-1}, R, D, W_L), \quad (5)$$

where θ_n is the bearing on which the animal arrives at location $\boldsymbol{x}_n$. We used different values of R corresponding roughly to the median distance traveled by caribou over the course of a day to over a week (R= 1500 m, 2000 m, 3000 m, 4000 m and 5000 m). We changed the grain of the habitat layer to consider overall availability of a habitat by taking its density in the circle of diameter D. We tested different values of smoothing using a range of diameters D, from 25 m (no smoothing) to 6000 m. We tested all combinations of R and D where $R - \frac{D}{2} \geq 1000\ m$ to assure independence in the estimation of local and long distance decisions. (Indeed, 95% of step lengths between consecutive 2-hour locations were <1000 m.)

This formulation allows us to compare different scenarios of complexity in movement decisions: (a) responses to local resources by using Equation (4); and (b) long-distance assessment of resources by using Equation (5). We used the Bayesian information criterion (BIC) to select the most parsimonious model given that we were interested in comparing models of finite-dimensionality (Yang 2005). To bolster our analysis, we examined resource use and selection on a seasonal scale (see Supplementary Appendix A). We calculated the maximum likelihood using the Nelder-Mead algorithm. All analyses were run with Python 2.7.5 and R 3.2.1.

Results

Model selection based on BIC revealed that all top models explicitly considered long-distance decisions (ΔBIC = 58,419, Table 1), implying that consideration of a general area over a relatively long distance is a better predictor of movement decisions than simply accounting for the resource type at the next recorded step – i.e. selection at the scale of the relocation data. The top model indicated that decisions based on a radius (R) of 2000 m and a smoothing diameter (D) of 2000 m outperformed other combinations of radius and smoothing (BIC = 536,299, Table 1) and was followed by other formulations involving relatively similar combinations of radius distance and smoothing grain size (Table 1). Nevertheless, combining the long-distance model based on $R = 2000$ and $D = 2000$ with the local model would lead to a model outperforming any assessment made at a single scale (ΔBIC = 35,046, Table 1). This indicates that movement in caribou is likely to result from decisions happening at multiple scales: i.e. that caribou balance both the proximate need to eat and the longer-scale requirement to move towards broad areas that are likely to provide sufficient forage for the days to come. A full list of candidate models is provided in Supporting Information.

Results for the local model (Table 2) are very similar to those reported in Potts et al. (2014); the negligible differences can be ascribed to removal of a few observations – i.e., missing data that arose when calculating the effect of resources at a longer distance. Results from the long-distance model (Table 2) indicated avoidance of dense coniferous habitat; this habitat was never attractive when caribou were in other habitat types and caribou were also strongly attracted to other habitats when in this habitat type (Table 2). This avoidance was much stronger at the long-distance scale than at the local scale, suggesting that avoidance of poor-quality habitat tends to be a long-term and broad-scale decision that may be harder to observe merely by examining successive 2-hourly telemetry locations (as is typical for step selection analysis).

Caribou also displayed preferences for open coniferous habitat in comparison to other habitats when modelled as making decisions over a long distance. This selection for coniferous open habitat was not apparent at the local scale. Caribou displayed a tendency to remain in barren or wetland habitats rather than switching between the two. This pattern is potentially indicative of two different movement modes associated with each habitat.

Our analysis of seasonal-scale resource selection - a longer scale than the either the short- or long-distance movement models - indicates that motion capabilities also affect caribou resource selection on a much larger spatio-temporal scale than the movement decisions of individuals (see Supplementary Appendix A). For "Other" and coniferous dense landcover, these seasonal-scale decisions play a strong role in the avoidance of these habitats (Table S1, Supplementary Appendix A), which bolsters observations made from analysis of the long-distance movement model.

Discussion

Using an extensive dataset of GPS telemetry locations from migratory caribou, we showed how animal movement can be described by assessing specific resources at both local and long-distances. Our novel movement model allows direct comparison between the long-distance model and the local model (described in Potts et al. 2014). This new model is particularly useful in uncovering avoidance of specific resources, such as coniferous dense forest. Such forest areas are known to be used by predators, such as coyotes and black bears (Bastille-Rousseau *et al.* 2015), so it is advantageous for caribou to stay a significant distance from this habitat type.

We observed that both models can be used to explain caribou movement, implying that movement-related decisions are taking place across multiple spatial and temporal scales but, more importantly, that the long-distance model performed better than the local model (Table 1). Comparing decisions made by caribou at the local and long-distance scales also showed opposite responses at each scale, a potential indication of the scale-specific trade-offs that caribou face. Overall, these results illustrate that the assumptions behind many movement models, related to scale in movement decisions, are unlikely to be upheld. We suggest that these findings may extend to a wide variety of animal species. Our work highlights the need to consider scale in resource decisions and overlapping behavioral processes in both movement modelling and data gathering (Schlägel and Lewis 2016a, b).

The field of movement ecology is teeming with new approaches to analyze our increasingly extensive fine-scale datasets of animal movement. Many of these approaches are based on random walk models of different complexities and include variable types of directional persistence or bias in animal movements (Benhamou 2014, Auger-Méthé et al. 2015). Many more models including mechanistic models of movement as well as the popular step-selection functions (Fortin et al. 2005) share a common methodological assumption – that the scale of decisions towards a specific resource is estimated at the scale of the GPS relocation. Recent studies are seeking to overcome this obstacle (Gautestad et al. 2013, Fleming et al. 2014, Blackwell et al. 2015). Our study represents part of the decades-long shift in ecology away from single, arbitrary scales in favor of multiple, animal-centered scales.

Frequency of GPS location acquisition is regularly specified as a trade-off to maximize transmitter battery life and onboard memory storage (Hebblewhite and Haydon 2010). Yet, the presence of long-term and shorter-term motivation potentially creates several levels of decisions that operate simultaneously to dictate animal movement and extend beyond most GPS telemetry studies (e.g. 2 days; Benhamou 2014). Consequently, assessing the effects of resources on movement solely at the scale of GPS-locations can be problematic, since observed movements are likely to be influenced by longer-distance considerations.

Another key consideration is the grain (Wheatley and Johnson 2009) at which animals may perceive and react to the environment. The importance of careful grain selection has received considerable attention in the field of habitat selection (Laforge et al. 2015a, 2015b), but its importance in animal movement models is much less frequently discussed. While we did not explicitly modify the grain of our landcover data, our models potentially indicate a similar importance of grain in movement modelling while also revealing biological insights for caribou.

We found that caribou selected open areas, including open coniferous and wetland habitats (Table 2), which is consistent with predator avoidance in this species (Valeix et al. 2009). Additional benefits from using open habitat include reducing biting insect harassment (Bergerud et al. 2008). In our study area, open habitats also offered the highest amount of forage to caribou (Bastille-Rousseau et al. 2015). Interestingly, caribou did not select coniferous open at a long-distance, despite being the most heavily used habitat. Simulated movement based on caribou step length and turning angle distribution and actual locations showed similar use and selection for this resource. While caribou are more likely to move to barren and wetland habitat at the local scale, at the larger scale they tend to be attracted toward areas containing coniferous open habitat types. This indicates that, while caribou actively select these stands, they likely select them for a very specific reason, such as foraging (Bastille-Rousseau et al. 2015). Such discrepancies between local and long-distance considerations also indicate how selection can be scale-sensitive.

We surmise that the long-distance model plays a stronger role for the conditions that caribou avoid, such as coniferous dense, than habitats that caribou select for. Indeed, it is likely that our long-distance model is more appropriate to detect avoidance than selection given that there are uncertainties as to whether circle C is used by caribou. Simulations based on the correlated random walk model also predicted selection for these habitats (Appendix A), further indicating that avoidance rather emerges because these habitats are rarely attractive at the local and long distance scale, in comparison to other habitats. While selection for barren habitat could be explained almost uniquely by the motion capacity of caribou, long-distance selection seems to play a role in the selection of barren habitat. Interestingly, caribou in barren or wetland habitat are likely to remain in the same habitat. This could potentially lead to negative edge effects between neighboring patches of these habitats (Potts et al. 2015).

Many species, including caribou, are known for their philopatry toward calving or reproductive areas (Gibson and Mann 2008, Schaefer and Mahoney 2013). Our work provides insight into how animals respond to their surroundings at a finer scale. We found that caribou are able to direct their movements to areas containing specific resources and that decisions are conditional upon where caribou are currently located. Within the extent of distances we sampled to represent long-distance decisions, 2000 m best represented caribou movement. This indicates that our study animals directed their movement towards areas that could be accessed roughly within 2-days travel distance. Such decisions are likely to extend beyond what caribou currently perceive of their environment, implying that caribou use a cognitive map of their surroundings to inform their foraging decisions (Fagan et al. 2013).

Our work adds to the increasing evidence of high-level cognitive processes (e.g., memory and orientation) in ungulates (Wolf et al. 2009, Gautestad et al. 2013, Merkle et al. 2014, Avgar et al. 2015). More importantly, our work shows that the scales at which resources affect movement and the grain of spatial data should be carefully selected. For female caribou, the long-distance model alone appears to be more salient than the local-distance model. In contrast, the arbitrary scale provided by GPS locations is likely to be unsuitable to reliably estimate meaningful responses to specific resources, meaning that approaches applied across scales (or combining decisions over multiple scales) are more likely to yield representative models of animal movement. As in many other facets of ecology, explicit consideration of scale in movement analysis is an inescapable priority for robust inference.

Acknowledgements

This study was funded by the Institute for Biodiversity, Ecosystem Science & Sustainability and the Sustainable Development & Strategic Science Division of the Newfoundland & Labrador Department of Environment & Conservation and also the Safari Club International Foundation. MAL gratefully acknowledges an NSERC Discovery Grant and Canada Research Chair. We thank J.-M. Gaillard, N. Morellet and an anonymous reviewer for providing comments on an earlier version of this manuscript. We thank the Department of Environment & Conservation for generating the telemetry data and we gratefully acknowledge the government personnel involved in caribou captures and monitoring over 4 decades. We thank K. Morgan, F. Norman and K. Lewis for preparing the telemetry data.

References

Auger-Méthé, M. et al. 2015. Differentiating the Lévy walk from a composite correlated random walk (L Börger, Ed.). - Methods Ecol. Evol. 6: 1179–1189.

Avgar, T. et al. 2013. An empirically parameterized individual based model of animal movement, perception, and memory. - Ecol. Modell. 251: 158–172.

Avgar, T. et al. 2015. Space-use behavior of woodland caribou based on a cognitive movement model. - J. Anim. Ecol. 84: 1059–1070.

Avgar, T. et al. 2016. Integrated step selection analysis: bridging the gap between resource selection and animal movement. - Methods Ecol. Evol. 7: 619–630.

Bastille-Rousseau, G. et al. 2015. Unveiling trade-offs in resource selection of migratory caribou using a mechanistic movement model of availability. - Ecography 38: 1049–1059.

Bastille-Rousseau, G. et al. 2016. Phase-dependent climate-predator interactions explain three decades of variation in neonatal caribou survival. - J. Anim. Ecol. 85: 445–456.

Benhamou, S. 2014. Of scales and stationarity in animal movements. - Ecol. Lett.: 261–272.

Bergerud, A. T. et al. 2008. The return of caribou to Ungava. - McGill-Queen's University Press.

Bergman, C. M. et al. 2000. Caribou movement as a correlated random walk. - Oecologia 123: 364–374.

Blackwell, P. G. et al. 2015. Exact Bayesian inference for animal movement in continuous time. - Methods Ecol. Evol. 7: 184–195.

Environment Canada 2013. National Climate Data and Information Archive. 2013

Fagan, W. F. et al. 2013. Spatial memory and animal movement. - Ecol. Lett. 16: 1316–1329.

Farnsworth, K. D. and Beecham, J. A. 1999. How do grazers achieve their distribution? A continuum of models from random diffusion to the ideal free distribution using biased random walks. - Am. Nat. 153: 509–526.

Fleming, C. H. et al. 2014. From Fine-Scale Foraging to Home Ranges: A Semivariance Approach to Identifying Movement Modes across Spatiotemporal Scales. - Am. Nat. 183: E154–E167.

Forester, J. D. et al. 2009. Accounting for animal movement in estimation of resource selection functions: sampling and data analysis. - Ecology 90: 3554–3565.

Fortin, D. et al. 2005. Wolves influence elk movements: Behavior shapes a trophic cascade in

Yellowstone National Park. - Ecology 86: 1320–1330.

Fortin, D. et al. 2013. Movement responses of caribou to human-induced habitat edges lead to their aggregation near anthropogenic features. - Am. Nat. 181: 827–836.

Fortin, D. et al. 2015. A spatial theory for characterizing predator–multiprey interactions in heterogeneous landscapes. - Proc. R. Soc. B Biol. Sci. 282: 20150973.

Gautestad, A. O. et al. 2013. Inferring spatial memory and spatiotemporal scaling from GPS data: comparing red deer Cervus elaphus movements with simulation models. - J. Anim. Ecol. 82: 572–586.

Gibson, Q. A. and Mann, J. 2008. The size, composition and function of wild bottlenose dolphin (Tursiops sp.) mother–calf groups in Shark Bay, Australia. - Anim. Behav. 76: 389–405.

Hebblewhite, M. and Haydon, D. T. 2010. Distinguishing technology from biology: a critical review of the use of GPS telemetry data in ecology. - Philos. Trans. R. Soc. B Biol. Sci. 365: 2303–2312.

Holyoak, M. et al. 2008. Trends and missing parts in the study of movement ecology. - Proc. Natl. Acad. Sci. U. S. A. 105: 19060–5.

Laforge, M. P. et al. 2015a. Process-focussed, multi-grain resource selection functions. - Ecol. Modell. 305: 10–21.

Laforge, M. P. et al. 2015b. Grain-dependent functional responses in habitat selection. - Landsc. Ecol. 31: 855–863.

Langrock, R. et al. 2012. Flexible and practical modeling of animal telemetry data: hidden Markov models and extensions. - Ecology 93: 2336–2342.

Merkle, J. A. et al. 2014. A memory-based foraging tactic reveals an adaptive mechanism for restricted space use (G Grether, Ed.). - Ecol. Lett. 17: 924–931.

Moorcroft, P. R. and Lewis, M. A. 2006. Mechanistic home range analysis. - Princeton University Press.

Morales, J. M. et al. 2005. Adaptive models for large herbivore movements in heterogeneous landscapes. - Landsc. Ecol. 20: 301–316.

Nathan, R. et al. 2008. A movement ecology paradigm for unifying organismal movement research. - Proc. Natl. Acad. Sci. U. S. A. 105: 19052–19059.

Potts, J. R. and Lewis, M. A. 2016. How memory of direct animal interactions can lead to territorial pattern formation. - J. R. Soc. Interface in press.

Potts, J. R. et al. 2014. Predicting local and non-local effects of resources on animal space use using a mechanistic step selection model. - Methods Ecol. Evol. 5: 253–262.

Potts, J. R. et al. 2015. The “edge effect” phenomenon: deriving population abundance patterns from individual animal movement decisions. - Theor. Ecol. in press.

Schaefer, J. A. and Mahoney, S. P. 2013. Spatial dynamics of the rise and fall of caribou (Rangifer tarandus) in Newfoundland. - Can. J. Zool. 91: 767–774.

Schlägel, U. E. and Lewis, M. A. 2014. Detecting effects of spatial memory and dynamic information on animal movement decisions (L Börger, Ed.). - Methods Ecol. Evol. 5: 1236–1246.

Schlägel, U. E. and Lewis, M. A. 2016a. Robustness of movement models: can models bridge the gap between temporal scales of data sets and behavioural processes? - J. Math. Biol. in press.

Schlägel, U. E. and Lewis, M. A. 2016b. A framework for analyzing the robustness of movement models to variable step discretization. - J. Math. Biol. in press.

Sikes, R. S. and Gannon, W. L. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. - J. Mammal. 92: 235–253.

Smouse, P. E. et al. 2010. Stochastic modelling of animal movement. - Philos. Trans. R. Soc. B Biol. Sci. 365: 2201–2211.

Sutherland, W. J. et al. 2013. Identification of 100 fundamental ecological questions (D Gibson, Ed.). - J. Ecol. 101: 58–67.

Turchin, P. 1998. Quantitative Analysis of Movement:Measuring and Modeling Population Redistribution in Animals and Plants. - Beresta Books.

Valeix, M. et al. 2009. Behavioral adjustments of African herbivores to predation risk by lions: Spatiotemporal variations influence habitat use. - Ecology 90: 23–30.

Van Moorter, B. et al. 2009. Memory keeps you at home: a mechanistic model for home range emergence. - Oikos 118: 641–652.

Wheatley, M. and Johnson, C. 2009. Factors limiting our understanding of ecological scale. - Ecol. Complex. 6: 150–159.

Wolf, M. et al. 2009. The attraction of the known: the importance of spatial familiarity in habitat selection in wapiti Cervus elaphus. - Ecography 32: 401–410.

Yang, Y. 2005. Can the strengths of AIC and BIC be shared? A conflict between model indentification and regression estimation. - Biometrika 92: 937–950.

Tables

Table 1. Top candidate models estimating a local or long distance responses to resources. Models differed in the radius R and grain size D (Figure 1) regarding how the long-distance model was estimated. Models were ranked based on BIC and ω BIC. Note that the model including both local and long distance responses was estimated by combining model ranked 1 and 30.

Rank	Attraction	R	D	BIC	ω BIC
1	Long	2000	2000	563299	1
2	Long	2000	1500	566523	0
3	Long	1500	500	572169	0
4	Long	2000	1000	572841	0
5	Long	3000	3000	574044	0
6	Long	4000	6000	576693	0
7	Long	2000	750	578703	0
8	Long	3000	2000	579260	0
9	Long	5000	6000	580154	0
10	Long	1500	350	581407	0
30	Local	-	-	621718	0
-	Both	2000	2000	528253	-

Table 2. Local and long-distance responses to resources for 140 female caribou in Newfoundland. Coefficients are derived from the top model (Table 1) based on a long-distance model of 2000 m and a smoothing diameter of 2000 m. Coefficients >1 represent attraction toward a specific habitat based on the presently occupied habitat; coefficient <1 represents avoidance.

	Local scale					Long-distance scale				
To	Barren	Wetland	Other	CD[1]	CO[2]	Barren	Wetland	Other	CD[1]	CO[2]
From										
Barren	1.000	1.058	0.403	0.635	0.884	1.000	0.635	<0.001	<0.001	1.280
Wetland	0.968	1.000	0.376	0.646	0.940	0.254	1.000	0.020	<0.001	1.397
Other	1.640	1.621	1.000	0.900	1.346	2.277	4.006	1.000	<0.001	11.453
CD[1]	1.159	1.091	0.351	1.000	1.062	>1000	>1000	>1000	1.000	>1000
CO[2]	1.075	1.071	0.283	0.822	1.000	0.047	0.030	0.041	<0.001	1.000

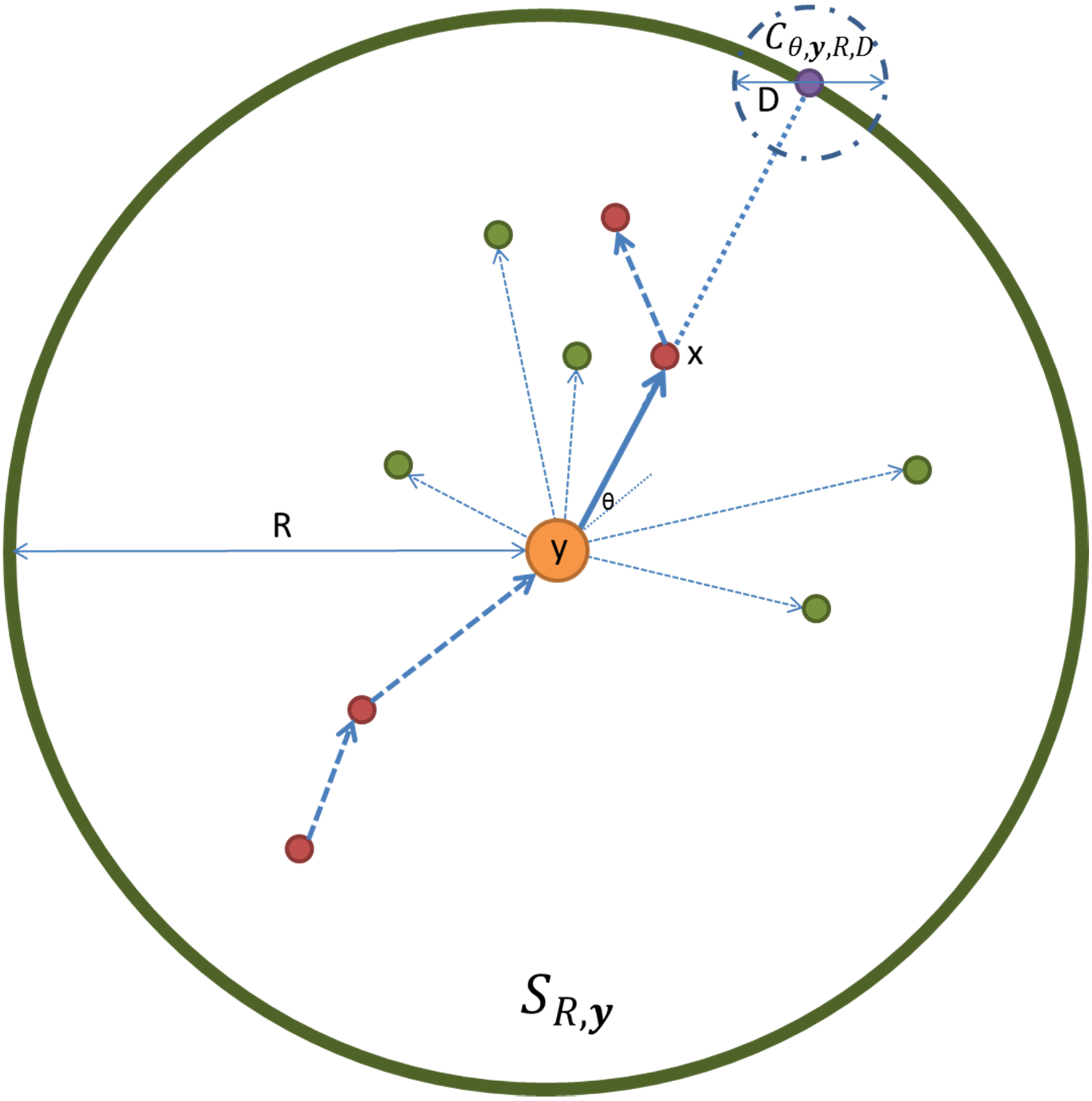
[1] Coniferous dense

[2] Coniferous open

Figure captions

Figure 1. Schematic sampling design for the estimation of local and long-distance responses to resources. Sequential animal locations are represented by red dots, the present location by the yellow point, y. *When moving from* y *to* x*, an animal can select or avoid local resources at* x *or resources centered at* C *(blue dots) at a distance* R. *Local decisions are estimated by comparing attributes at* x *with attributes at locations that could have been reached over the same period (green dots). Long-distance decisions is estimated by comparing attributes in* C *with attributes found within the bigger circle of radius* R.

451 **Figure 1.**



452