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

3

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21

22 **Abstract**

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

38

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

41 **Introduction**

42 Understanding organism movement is a fundamental challenge in ecology (Sutherland et al.  
43 2013). The movements of animals influence ecological processes operating at multiple spatial  
44 and temporal scales (Nathan et al. 2008), with repercussions for individual fitness as well as  
45 population, community, and ecosystem function (Turchin 1998, Holyoak et al. 2008, Fortin et al.  
46 2015). Nathan et al. (2008) proposed a unifying paradigm of an organism's movement derived  
47 from interactions with the environment, its internal state, and mechanical and navigational  
48 properties of the organism. Moreover, realistic modelling of animal movement often needs to be  
49 applied at biologically-relevant scales, sometimes multiple scales. This can represent a daunting  
50 task for ecologists, owing to the highly dynamic interactions of organisms with their  
51 environment and internal state. Mechanical-navigational properties alone may offer limited  
52 insight into the determinants of animal movement.

53 Lagrangian models are useful for generating multi-segment trajectories of animal  
54 movement, akin to information typically acquired from satellite telemetry (Smouse et al. 2010).  
55 Simpler expressions of these models, such as random walks, assume little navigation capacities,  
56 but focus extensively on the motion capacity of animals by fitting a specific step-length  
57 distribution (Turchin 1998). More complex expressions, such as correlated random walk or  
58 biased random walk models, integrate navigational capacities by adding persistence in movement  
59 or attraction to specific area, respectively (Farnsworth and Beecham 1999, Bergman et al. 2000).  
60 When combined with information about the landscape and resource distribution, random walk  
61 models can improve our understanding of resource selection and thereby generate more realistic  
62 patterns of space-use (Moorcroft and Lewis 2006, Smouse et al. 2010, Fortin et al. 2013, Potts et  
63 al. 2014, Bastille-Rousseau et al. 2015). Indeed, it seems that most movement behavior can be

64 reproduced by a mixture of random walk models operating at different scales (Benhamou 2014).  
65 Therefore, by building on these developments, ecologists can focus more on understanding the  
66 factors driving navigational process, including elements related to orientation, memory, and the  
67 formulation of a cognitive map by an animal (Van Moorter et al. 2009, Avgar et al. 2013, Fagan  
68 et al. 2013, Merkle et al. 2014, Schlägel and Lewis 2014, Potts and Lewis 2016).

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

81         Furthermore, navigational abilities may be driven by behavioral processes operating at  
82 different spatio-temporal scales (Fleming et al. 2014, Benhamou 2014). For instance, a migrating  
83 animal might orient its fine-scale movements toward habitat that provides foraging opportunities  
84 or low mortality risk, while ignoring habitat that has higher costs. Whereas these two processes –  
85 migration and interpatch movement – operate at distinct scales and can be represented  
86 independently (Benhamou 2014), an animal’s motivations related to migratory and interpatch

87 movements likely compete in generating the observed distributions of step length, turning angle  
88 and habitat use, as captured by telemetry. Observations at the arbitrary scale of telemetry data  
89 could fail to capture decisions happening at either scale. The role of memory and cognition have  
90 been at the forefront of recent movement modelling (Van Moorter et al. 2009, Avgar et al. 2013,  
91 2015, Fagan et al. 2013, Potts and Lewis 2016), but it remains unclear how differing spatio-  
92 temporal scales lead to variability in animal interactions with resources.

93         Here, we investigated the importance of decisions relative to environmental resources in  
94 animal movement and how its estimation can be influenced by the scale at which it is assessed.  
95 We focused on the motion and navigational capacities of Newfoundland caribou (*Rangifer*  
96 *tarandus* L.) during the calving period and tested how movement can be explained by a mixture  
97 of local or long-distance responses to specific resources. There are fourteen major caribou herds  
98 inhabiting the island of Newfoundland, with most female caribou exhibiting spring migration to  
99 traditional calving grounds. We compared an approach inspired by the specific SSF framework  
100 of Potts et al. (2014), that considers decisions at the scale of the GPS relocations, to a new model  
101 of long-distance decisions that capture movement in the direction of areas that an animal could  
102 reach over many hours or days. To examine the effect of movement on seasonal scale behavior,  
103 we compared resource use and selection of caribou to predicted patterns of use and selection  
104 based on the motion capacity of caribou. We hypothesized that selection toward certain resources  
105 and avoidance of others would be necessary in order to explain movement of caribou because the  
106 habitat selection of female caribou during post-calving represents a tradeoff for minimizing  
107 predation risk (at the broad scale) and foraging (at the fine scale). Accordingly, we predicted that  
108 caribou movement would be best represented by assessing resource selection at a longer distance  
109 than the one provided by GPS relocations (Bastille-Rousseau et al. 2015). We believe that the

110 modelling framework proposed here will set the foundation for building predictive models of  
111 animal movement that are more reflective of realistic biological determinants, and thereby  
112 represent an improvement to traditional telemetry-based animal movement modeling.

113

## 114 **Methods**

### 115 Study area

116 Newfoundland is a 108,860-km<sup>2</sup> island at the eastern extremity of Canada (47°44N, 59°28W -  
117 51°44N, 52°38W), with humid-continental climate and substantial year-round precipitation  
118 (Environment Canada 2013). Natural habitat consists mainly of coniferous and mixed forests of  
119 balsam fir (*Abies balsamea*), black spruce (*Picea mariana*), and white birch (*Betula papyrifera*)  
120 and, in some locations, substantial areas composed of bogs and heath or barren habitats. Our  
121 analyses were based on Landsat TM satellite imagery, with a resolution of 25 m, classified into 5  
122 different habitat types: wetland habitats (Wetland), barren and other open habitats (Barren),  
123 mixed and coniferous open stand (CO), mixed and coniferous dense stand (CD), open water and  
124 other rarer habitats such as broadleaf stands, herbs and bryoids (Other) (Wulder et al. 2008).  
125 Anthropogenic disturbances were not extensive on these caribou ranges and consisted of logging,  
126 hydroelectric developments, and roads. We restricted our analysis to five important migratory  
127 herds located south of the main east-west highway that crossed the island.

128

### 129 Animal capture and monitoring

130 During 2006-2010, more than 200 caribou were captured, principally during winter, and fitted  
131 with global positioning system (GPS) collars that obtained locations every 2 hours. We focused  
132 on 140 adult females (361 caribou-years and 371,744 locations), 2006-2012, that resided in 6

133 herds. We limited our movement analysis to the crucial, post-migratory period of calving and  
134 post-calving (1 May - 1 August) when most caribou neonate mortalities occur (Bastille-Rousseau  
135 et al. 2016). All animal capture and handling procedures were consistent with the American  
136 Society of Mammologists guidelines (Sikes and Gannon 2011).

137

138 Statistical analyses

139 In Potts *et al.* (2014), a method was developed for inferring the probability of finding a caribou  
140 in a habitat  $H(\mathbf{x})$ , given that it was at position  $\mathbf{y}$  in the previous step (2 hours previously) and  
141 arrived there on a trajectory  $\theta_0$ . The model takes the form:

$$142 \quad P_S(H(\mathbf{x})|\mathbf{y}, \theta_0, W_S) = K_S(\mathbf{y}, \theta_0)^{-1}\{A_S(H(\mathbf{x})|\mathbf{y}, \theta_0)W_S[H(\mathbf{x}), H(\mathbf{y})]\} \quad (1)$$

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

151  $\int_{\Omega} P_S(H(\mathbf{x})|\mathbf{y}, \theta_0, W_S)d\mathbf{x} = 1$ , where  $\Omega$  is the study area.

152 A drawback of this approach is that it assumes caribou make movement decisions on a 2-  
153 hour framework. In reality, since they have home ranges that are dozens of kilometers across,  
154 they are likely to make longer-scale decisions when moving. To test this hypothesis, we  
155 constructed a model describing probability of an animal moving towards a region of a given area



156 (defined based on the proportion of each landcover within a circle of diameter  $D$ ), at a distance  $R$   
 157 away from the animal, containing habitat of type  $i$  (see Figure 1). This model is:

$$158 \quad P_L(i|\mathbf{y}, R, D, W_L) = K_L(\mathbf{y}, R, D)^{-1} A_L(i|\mathbf{y}, R, D) W_L[i, H(\mathbf{y})], \quad (2)$$

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

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

$$176 \quad P_L(H_L(\theta)|\mathbf{y}, R, D, W_L) = K_L(\mathbf{y}, R, D)^{-1} \sum_{i \in \mathcal{H}} A_L(i|\mathbf{y}, R, D) Q(i|\theta, \mathbf{y}, R, D) W_L[i, H(\mathbf{y})]. \quad (3)$$

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

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

$$180 \quad L_S(\mathbf{x}_0, \mathbf{x}_1, \dots, \mathbf{x}_N | W_S) = \prod_{n=1}^N P_S(H(\mathbf{x}_n) | \mathbf{x}_{n-1}, \theta_{n-1}, W_S), \quad (4)$$

$$181 \quad L_L(\mathbf{x}_0, \mathbf{x}_1, \dots, \mathbf{x}_N | W_L) = \prod_{n=1}^N P_L(H_L(\theta_n) | \mathbf{x}_{n-1}, R, D, W_L), \quad (5)$$

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

190 This formulation allows us to compare different scenarios of complexity in movement  
191 decisions: (a) responses to local resources by using Equation (4); and (b) long-distance  
192 assessment of resources by using Equation (5). We used the Bayesian information criterion  
193 (BIC) to select the most parsimonious model given that we were interested in comparing models  
194 of finite-dimensionality (Yang 2005). To bolster our analysis, we examined resource use and  
195 selection on a seasonal scale (see Supplementary Appendix A). We calculated the maximum  
196 likelihood using the Nelder-Mead algorithm. All analyses were run with Python 2.7.5 and R  
197 3.2.1.

198

199 **Results**

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

214 Results for the local model (Table 2) are very similar to those reported in Potts et al.  
215 (2014); the negligible differences can be ascribed to removal of a few observations – i.e., missing  
216 data that arose when calculating the effect of resources at a longer distance. Results from the  
217 long-distance model (Table 2) indicated avoidance of dense coniferous habitat; this habitat was  
218 never attractive when caribou were in other habitat types and caribou were also strongly attracted  
219 to other habitats when in this habitat type (Table 2). This avoidance was much stronger at the  
220 long-distance scale than at the local scale, suggesting that avoidance of poor-quality habitat tends  
221 to be a long-term and broad-scale decision that may be harder to observe merely by examining  
222 successive 2-hourly telemetry locations (as is typical for step selection analysis).

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

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

235

## 236 **Discussion**

237 Using an extensive dataset of GPS telemetry locations from migratory caribou, we showed how  
238 animal movement can be described by assessing specific resources at both local and long-  
239 distances. Our novel movement model allows direct comparison between the long-distance  
240 model and the local model (described in Potts et al. 2014). This new model is particularly useful  
241 in uncovering avoidance of specific resources, such as coniferous dense forest. Such forest areas  
242 are known to be used by predators, such as coyotes and black bears (Bastille-Rousseau *et al.*  
243 2015), so it is advantageous for caribou to stay a significant distance from this habitat type.

244 We observed that both models can be used to explain caribou movement, implying that  
245 movement-related decisions are taking place across multiple spatial and temporal scales but,

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

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

264         Frequency of GPS location acquisition is regularly specified as a trade-off to maximize  
265 transmitter battery life and onboard memory storage (Hebblewhite and Haydon 2010). Yet, the  
266 presence of long-term and shorter-term motivation potentially creates several levels of decisions  
267 that operate simultaneously to dictate animal movement and extend beyond most GPS telemetry  
268 studies (e.g. 2 days; Benhamou 2014). Consequently, assessing the effects of resources on

269 movement solely at the scale of GPS-locations can be problematic, since observed movements  
270 are likely to be influenced by longer-distance considerations.

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

277 We found that caribou selected open areas, including open coniferous and wetland  
278 habitats (Table 2), which is consistent with predator avoidance in this species (Valeix et al.  
279 2009). Additional benefits from using open habitat include reducing biting insect harassment  
280 (Bergerud et al. 2008). In our study area, open habitats also offered the highest amount of forage  
281 to caribou (Bastille-Rousseau et al. 2015). Interestingly, caribou did not select coniferous open at  
282 a long-distance, despite being the most heavily used habitat. Simulated movement based on  
283 caribou step length and turning angle distribution and actual locations showed similar use and  
284 selection for this resource. While caribou are more likely to move to barren and wetland habitat  
285 at the local scale, at the larger scale they tend to be attracted toward areas containing coniferous  
286 open habitat types. This indicates that, while caribou actively select these stands, they likely  
287 select them for a very specific reason, such as foraging (Bastille-Rousseau et al. 2015). Such  
288 discrepancies between local and long-distance considerations also indicate how selection can be  
289 scale-sensitive.

290 We surmise that the long-distance model plays a stronger role for the conditions that  
291 caribou avoid, such as coniferous dense, than habitats that caribou select for. Indeed, it is likely

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

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

311 Our work adds to the increasing evidence of high-level cognitive processes (e.g., memory  
312 and orientation) in ungulates (Wolf et al. 2009, Gautestad et al. 2013, Merkle et al. 2014, Avgar  
313 et al. 2015). More importantly, our work shows that the scales at which resources affect  
314 movement and the grain of spatial data should be carefully selected. For female caribou, the

315 long-distance model alone appears to be more salient than the local-distance model. In contrast,  
316 the arbitrary scale provided by GPS locations is likely to be unsuitable to reliably estimate  
317 meaningful responses to specific resources, meaning that approaches applied across scales (or  
318 combining decisions over multiple scales) are more likely to yield representative models of  
319 animal movement. As in many other facets of ecology, explicit consideration of scale in  
320 movement analysis is an inescapable priority for robust inference.

321

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425

426

427 **Tables**

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

<b>Rank</b>	<b>Attraction</b>	<b>R</b>	<b>D</b>	<b>BIC</b>	<b><math>\omega</math> BIC</b>
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	-

433

434

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

	Local scale					Long-distance scale					
	To	Barren	Wetland	Other	CD <sup>1</sup>	CO <sup>2</sup>	Barren	Wetland	Other	CD <sup>1</sup>	CO <sup>2</sup>
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 <sup>1</sup>	1.159	1.091	0.351	1.000	1.062	>1000	>1000	>1000	1.000	>1000	
CO <sup>2</sup>	1.075	1.071	0.283	0.822	1.000	0.047	0.030	0.041	<0.001	1.000	

440 <sup>1</sup> Coniferous dense

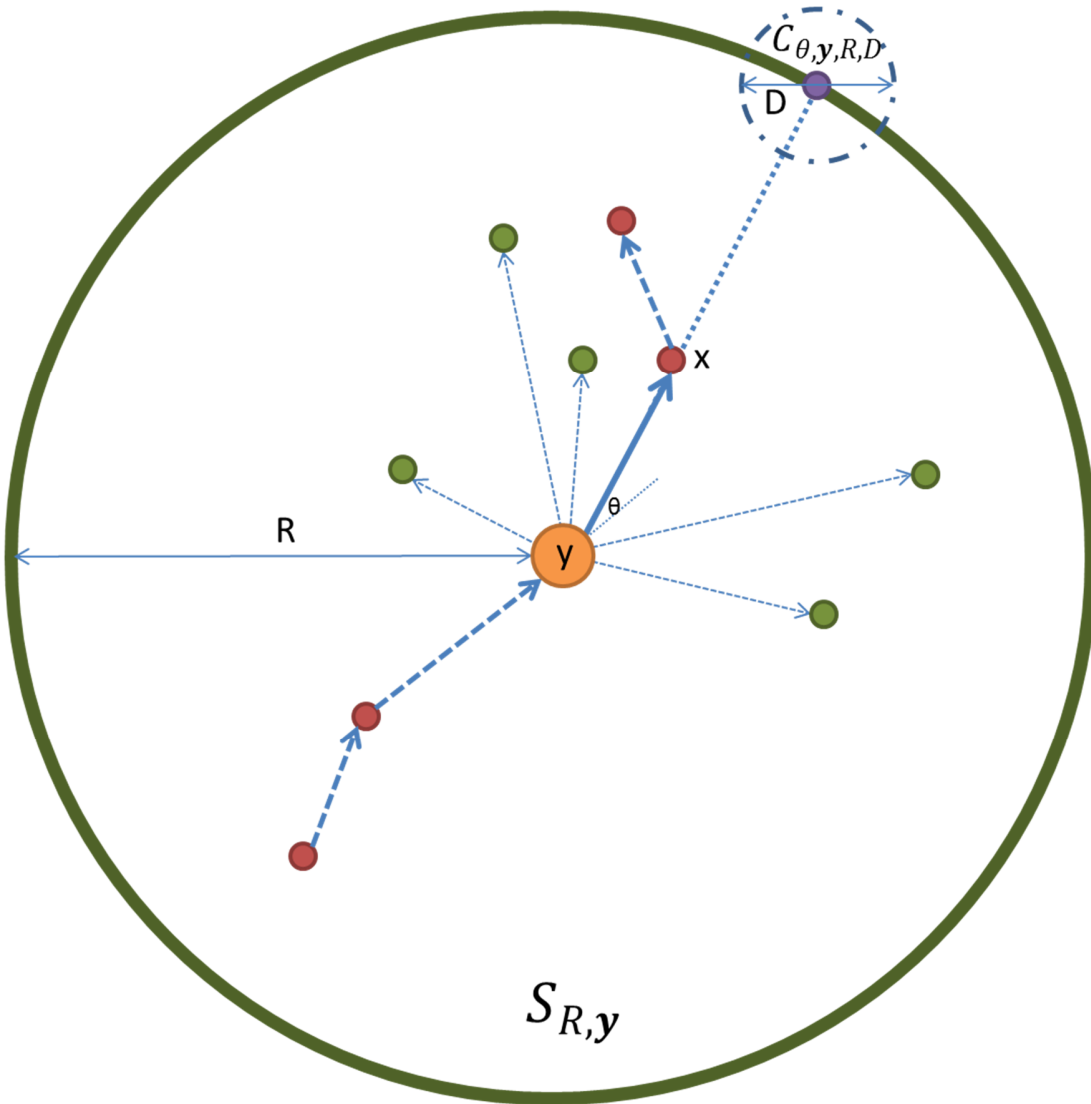
441 <sup>2</sup> Coniferous open

442

443 **Figure captions**

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

451 **Figure 1.**



452