

1 Evaluating random search strategies in three mammals  
2 from distinct feeding guilds

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## 14 Summary

- 15 1. Searching allows animals to find food, mates, shelter, and other resources essential for  
16 survival and reproduction, and is thus among the most important activities  
17 performed by animals. Theory predicts that animals will use random search  
18 strategies in highly variable and unpredictable environments. Two prominent models  
19 have been suggested for animals searching in sparse and heterogeneous environments:  
20 (i) the Lévy walk and (ii) the composite correlated random walk (CCRW) and its  
21 associated area-restricted search behaviour. Until recently, it was difficult to  
22 differentiate between the movement patterns of these two strategies.
  
- 23 2. Using a new method that assesses whether movement patterns are consistent with  
24 these two strategies and two other common random search strategies, we investigated  
25 the movement behaviour of three species inhabiting sparse northern environments:  
26 woodland caribou (*Rangifer tarandus caribou*), barren ground grizzly bear (*Ursus*  
27 *arctos*), and polar bear (*U. maritimus*). These three species vary widely in their  
28 diets, and thus allow us to contrast the movement patterns of animals from different  
29 feeding guilds.
  
- 30 3. Our results showed that, although more traditional methods would have found  
31 evidence for the Lévy walk for some individuals, a comparison of the Lévy walk to  
32 CCRWs showed stronger support for the latter. While a CCRW was the best model  
33 for most individuals, there was a range of support for its absolute fit. A CCRW was  
34 sufficient to explain the movement of nearly half of herbivorous caribou and a quarter  
35 of omnivorous grizzly bears, but was insufficient to explain the movement of all  
36 carnivorous polar bears.

37 4. Strong evidence for CCRW movement patterns suggests that many individuals may  
38 use a multiphasic movement strategy rather than one-behaviour strategies such as the  
39 Lévy walk. The fact that the best model was insufficient to describe the movement  
40 paths of many individuals suggests that some animals living in sparse environments  
41 may use strategies that are more complicated than those described by the standard  
42 random search models. Thus, our results indicate a need to develop movement models  
43 that incorporate factors such as the perceptual and cognitive capacities of animals.

#### 44 **Keywords**

45 Animal movement, Arctic, Area-concentrated search, Hidden Markov model, Lévy flight,  
46 Optimal foraging theory, Telemetry

### 47 **1 Introduction**

48 Searching is among an animal's most important activities as it provides the means to find  
49 food, mates, shelter, and other resources essential for survival and reproduction (Bell,  
50 1991). Search efficiency will affect performance and fitness, and thus we expect animals to  
51 use movement strategies that minimise the costs of locating resources (Zollner & Lima,  
52 1999; Conradt *et al.*, 2003). The importance of this behaviour has driven ecologists to  
53 focus on animals' search strategies (e.g., Bell, 1991; Benhamou, 1994; Viswanathan *et al.*,  
54 1999), and the recent increase in the availability of movement data has allowed this field to  
55 flourish (e.g., Fauchald & Tveraa, 2003; Nevitt, Losekoot & Weimerskirch, 2008;  
56 Humphries *et al.*, 2010). One focus has been to assess whether animals use the search  
57 strategies that theory predicts will be optimal in their environments (e.g.,  
58 Humphries *et al.*, 2010; Sims *et al.*, 2012). Using movement data for this assessment  
59 remains challenging because the efficiency of search strategies changes over environmental

60 gradients and the movement patterns they produce can be difficult to differentiate  
61 (Zollner & Lima, 1999; Bartumeus *et al.*, 2002; Benhamou, 2007; Plank & Codling, 2009).  
62 The efficacy of movement strategies are dependent on the variability and predictability of  
63 resource distributions. When resources are unpredictable in space and time, random search  
64 strategies are expected to emerge (Mueller & Fagan, 2008). Although animals are known  
65 to use perceptual cues to detect nearby resources, empiricists have found support for the  
66 use of random search strategies (e.g., Humphries *et al.*, 2010; Sims *et al.*, 2012). Theorists  
67 have proposed a set of random search strategies that are thought to be optimal under  
68 different conditions. While simple Brownian motion may be sufficient in productive areas,  
69 the Lévy walk may be advantageous in sparse environments because its rare, extremely  
70 long steps enable animals to explore new areas (Bartumeus *et al.*, 2002; Humphries *et al.*,  
71 2010, but see James, Plank & Edwards 2011; Benhamou & Collet 2015; Pyke 2015).  
72 Relative to Brownian motion, the Lévy walk is increasingly efficient with decreasing food  
73 density (Viswanathan *et al.*, 1999; Bartumeus *et al.*, 2002). When food density is low, the  
74 Lévy walk is also more efficient than a correlated random walk (Bartumeus *et al.*, 2005).  
75 The correlated random walk is a search strategy characterised by nearly straight movement  
76 that was shown to be efficient at finding sparsely distributed patches (Zollner & Lima,  
77 1999). The composite correlated random walk (CCRW) is a two-behaviour strategy that is  
78 more efficient than single-behaviour models in heterogeneous landscapes  
79 (Knoppien & Reddingius, 1985; Benhamou, 1992; Plank & James, 2008;  
80 Benhamou & Collet, 2015). The ‘extensive’ phase of the CCRW uses the nearly straight  
81 movement that makes the correlated random walk efficient at finding patches. The  
82 discovery of a food item triggers the ‘intensive’ phase, which is characterised by slower,  
83 more tortuous movement and sometimes referred as area-restricted search. These two

84 behavioural phases allow animals to adjust their movement according to local food density  
85 and the intensive phase enables them to stay within patches, even when patches have no  
86 perceptible boundaries (Knoppien & Reddingius, 1985; Benhamou, 1992). Many  
87 environments are sparse, heterogeneous, and unpredictable. While Brownian motion and  
88 correlated random walk might be insufficient in these instances, both the Lévy and CCRW  
89 may be advantageous random search strategies.

90 While the underlying searching behaviours of the Lévy and CCRW strategies differ, their  
91 movement patterns are similar and difficult to differentiate (Benhamou, 2007;  
92 Plank & Codling, 2009; Auger-Méthé, Plank & Codling, 2014). However, new methods  
93 have been developed to distinguish between the movement patterns associated with these  
94 strategies (Plank, Auger-Méthé & Codling, 2013; Auger-Méthé *et al.*, 2015). Here, we  
95 investigated the movement of three mammals for evidence of patterns consistent with  
96 random search strategies. As detailed below, we chose these species because previous  
97 research or the nature of their environment suggests that they may use random search  
98 strategies. All are large and wide-ranging mammals inhabiting northern Canada. However,  
99 these species vary widely in their foraging behaviours, allowing us to contrast the  
100 movement behaviours of animals in different feeding guilds.

101 Our first study species is a large herbivore, the woodland caribou (*Rangifer tarandus*  
102 *caribou*). We studied them in winter, when resources are scarce and they may be more  
103 likely to use random search strategies (Adamczewski *et al.*, 1987;  
104 Parker, Barboza & Stephenson, 2005). Their movement was shown to be consistent with a  
105 two-behaviour model similar to the CCRW (Johnson *et al.*, 2002b), and a different  
106 subspecies was suggested to use the Lévy strategy (Mårell, Ball & Hofgaard, 2002). Thus,  
107 applying these newly available tools may help clarify how caribou search their environment.

108 Our second study organism is a large Arctic omnivore, the barren ground grizzly bear  
109 (*Ursus arctos*). Our study population inhabits an area of low productivity, the Mackenzie  
110 Delta, Northwest Territories, Canada (McLoughlin *et al.*, 1999). Unlike other grizzlies that  
111 rely on predictable sources of protein, such as salmon (*Oncorhynchus spp.*), the barren  
112 ground grizzlies of the Mackenzie Delta have a small body size and drifting home ranges  
113 (Hilderbrand *et al.*, 1999; Edwards, Nagy & Derocher, 2009). The benefits of familiarity  
114 are limited in scarce, heterogeneous, and unpredictable environments (Switzer, 1993;  
115 Mueller & Fagan, 2008), thus site fidelity was suggested to be maladaptive for these bears  
116 (Edwards, Nagy & Derocher, 2009). Thus, random search strategies may be effective for  
117 barren ground grizzlies, making these bears good candidate for our study.

118 Our third species, the polar bear (*U. maritimus*), is a specialised marine carnivore. Polar  
119 bears, like many other predators that have been the focus of search strategy studies,  
120 exploit the unpredictable marine environment (e.g., Humphries *et al.*, 2010, 2012, but see  
121 Regular, Hedd & Montevecchi 2013). Polar bears exhibit site fidelity  
122 (Mauritzen, Derocher & Wiig, 2001), which could encourage the use of memory-based  
123 search strategies. However, other species that exhibit site fidelity are also thought to use  
124 random search strategies or a mixture of memory and random search strategies (e.g.,  
125 Humphries *et al.*, 2012; Gautestad & Mysterud, 2013). Polar bears use the sea ice as a  
126 platform to hunt seals (Stirling & Derocher, 2012). Sea ice extent changes seasonally and  
127 local ice concentration can vary drastically over short time scales (Maslanik & Barry, 1989;  
128 Johannessen *et al.*, 2004), which may make random search strategies advantageous.  
129 Using data collected when these three species were expected to be searching for food, we  
130 investigated whether their movement patterns were consistent with one of these four  
131 random search strategies. To do so, we compared the relative fit of a set of models, each

132 representing the movement pattern of one of the search strategies. We then assessed the  
133 absolute fit of the best model to verify whether it described the observed movement well.

## 134 **2 Materials and methods**

### 135 **2.1 Modeling search strategies**

136 We used the method described in Auger-Méthé *et al.* (2015) to assess whether the  
137 movement patterns of three species were consistent with a set of search strategies. This  
138 method defines likelihood functions that model the movement pattern of each of the four  
139 search strategies (Table 1), and can be considered a generalised and statistically rigorous  
140 extension of earlier methods. Each likelihood function was applied to the time series of  
141 step lengths,  $l_t$ , and turning angles,  $\theta_t$ , of each individual. The movement pattern of Lévy  
142 strategy was represented by a truncated Lévy walk (TLW), which used a truncated Pareto  
143 distribution for the step length,  $\psi_T(l)$ , and a circular uniform distribution for the turning  
144 angle,  $v_0(\theta)$  (Table 2). The movement pattern of the Brownian motion was represented by  
145 a Brownian walk (BW), which used an exponential distribution for the step length,  $\phi_T(l)$ ,  
146 and a circular uniform distribution for the turning angle,  $v_0(\theta)$  (Table 2). The correlated  
147 random walk (CRW) also used an exponential distribution for the step length,  $\phi_T(l)$ , but in  
148 combination with a von Mises distribution centred at 0 for the turning angle,  $v(\theta)$  (Table  
149 2). The CCRW version from Auger-Méthé *et al.* (2015), which we refer to as CCRW<sub>A</sub>, used  
150 a hidden Markov model with two movement behaviours (Table 1). The movement pattern  
151 of the intensive phase was represented by a Brownian walk with exponential distribution  
152 for the step length,  $\phi(l)$ , and a circular uniform distribution for the turning angle,  $v_0(\theta)$   
153 (Table 2). The movement pattern of the extensive phase was represented by a correlated  
154 random walk with an exponential distribution for the step length,  $\phi(l)$ , and a von Mises  
155 distribution centred at 0 for the turning angle,  $v(\theta)$  (Table 2). As we suggested in

156 Auger-Méthé *et al.* (2015), we also explored an additional version of the CCRW based on  
157 the hidden semi-Markov model presented in Langrock *et al.* (2012), which we refer as  
158 CCRW<sub>L</sub>. For this version, we used the same step length and turning angle distributions as  
159 in the CCRW<sub>A</sub>. However, the CCRW<sub>L</sub> used transition probabilities that depended on  
160 Poisson-distributed state dwell times rather than the fixed transition probabilities used in  
161 the CCRW<sub>A</sub> (Table 2).

162 We used maximum likelihood estimation to estimate the parameters of each model and the  
163 likelihood profile to estimate their confidence intervals (Bolker, 2008). To identify the  
164 model that best fit the movement data of each individual, the relative fit of these likelihood  
165 functions was assessed using the second-order Akaike information criterion ( $AIC_c$ ) and  
166 Akaike weights (Burnham & Anderson, 2002). Because the CCRW<sub>A</sub> and CCRW<sub>L</sub> were two  
167 models representing the movement pattern of the same search strategy, we summed their  
168 Akaike weights ( $w_{CCRW} = w_{CCRW_A} + w_{CCRW_L}$ ). We evaluated whether the best model  
169 adequately explained the movement data using a test of absolute fit, which consisted of a  
170 G-test on uniform pseudo-residuals (Sokal & Rohlf, 1981; Zucchini & MacDonald, 2009;  
171 Auger-Méthé *et al.*, 2015). All analyses were completed in R (R Core Team, 2015) and the  
172 code used to complete the analyses is available on Github  
173 (<https://github.com/MarieAugerMethe/CCRWvsLW/tree/v2.0>). See Auger-Méthé *et al.*  
174 (2015) for more detail.

## 175 **2.2 Description of movement data**

176 We used the movement data of three northern mammal species (data available on the  
177 University of Alberta Education & Research Archive:  
178 <https://era.library.ualberta.ca/>). To capture rare events, such as the long steps



179 characteristic of the Lévy walk, we attempted to get time series representing close to a year  
180 of movement behaviour. However, we also tried to limit the time series to movement  
181 performed while searching. As detailed below, we removed all sections of the datasets  
182 known to be associated with reproduction and resting, as the changes in movement  
183 patterns associated with such behaviours could affect our analyses (e.g., DeMars *et al.*,  
184 2013). We also started each time series a minimum of two weeks after the collaring event  
185 because capturing procedures associated with collaring affect the movement of some species  
186 (e.g., Morellet *et al.*, 2009; Thiemann *et al.*, 2013). The time series of some individuals  
187 were further reduced by missing observations and collar failures.

188 The first dataset included the movement paths of 22 female caribou from the boreal plains  
189 region of northeastern British Columbia, Canada. These females were captured during  
190 February and March 2011 and fitted with G2110E collars from Advanced Telemetry  
191 Systems Inc. (Isanti, MN, USA). The collars provided daily Global Positioning System  
192 (GPS) locations. We removed the calving and rut periods, as well as the two weeks post  
193 collaring, by limiting the time series to locations collected between November 1<sup>st</sup> 2011 to  
194 April 30<sup>th</sup> 2012 (Ferguson & Elkie, 2004). The second dataset included the movement  
195 paths of 20 grizzly bears from the Mackenzie Delta, Northwest Territories, Canada. These  
196 bears were collared in May and June (close to den emergence) 2003-2009. For each  
197 individual, we used locations collected during the first year after collaring, in the period  
198 between July 1<sup>st</sup> to November 30<sup>th</sup> (or den entrance). Starting July 1<sup>st</sup> excluded the peak  
199 of the mating season (MacHutchon, 1996) and the two weeks following the collaring events.  
200 The third dataset included the movement paths of 12 polar bears from the Beaufort Sea.  
201 These bears were collared in April and May 2008-2010. To exclude the two weeks after  
202 collaring, we started the time series June 1<sup>st</sup>. We used locations collected until the

203 subsequent June 1<sup>st</sup>. As some pregnant females of the Beaufort Sea give birth in dens on  
204 the moving sea ice (Amstrup & Gardner, 1994), it is difficult to identify den location. To  
205 exclude denning individuals, we included only juveniles and females accompanied with  
206 cubs-of-the-year or yearlings when collared. Restricting the analysis to these individuals  
207 also removed the potential for mating events in the time series. The locations of both the  
208 grizzly and polar bears are GPS locations taken every 4hrs with Gen II-IV collars from  
209 Telonics Inc. (Mesa, AZ, USA).

210 The collars of all of these animals were programmed to collect locations at regular time  
211 intervals. Transforming sampled steps into biologically relevant steps is among the most  
212 difficult challenges of using GPS data in ecology (Hebblewhite & Haydon, 2010), and  
213 various methods have been proposed (e.g., Codling & Plank, 2011). We chose to use the  
214 local turn method, a technique that creates one step out of all consecutive sampled steps  
215 with a turning angle smaller than a threshold angle (see Codling & Plank, 2011;  
216 Auger-Méthé *et al.*, 2015). This technique, as well as other similar methods, can cause the  
217 misidentification of CCRWs for Lévy walks (Codling & Plank, 2011;  
218 Plank, Auger-Méthé & Codling, 2013). However, misidentifications are more likely to occur  
219 when high threshold angles are used (Codling & Plank, 2011;  
220 Plank, Auger-Méthé & Codling, 2013). We chose a threshold angle of 10° because this  
221 small value limited the potential for misidentification and interpreted movement in the  
222 same general direction (i.e., any sampled step within the 20° forward sector) as part of a  
223 biologically relevant step (Auger-Méthé *et al.*, 2015). To verify that variations in threshold  
224 angles did not affect the results, we also explored a range of threshold angles. We show in  
225 Appendix S1 that the results were broadly similar regardless of the threshold angle used.  
226 Note that this local turn method can impact the test of absolute fit based on turning angle

227 distribution (Auger-Méthé *et al.*, 2015), and we presented only the test of absolute fit for  
228 the step length distribution. Because missing locations can affect steps defined by the local  
229 turn method, we included only individuals that had a time series with < 30% of the  
230 locations missing. We also limited the time series to those with a minimum of 50 steps  
231 (Appendix S2 presents the range of sample size). We applied the models to the data from  
232 each individual separately.

### 233 **3 Results**

234 According to  $AIC_c$ , one of the CCRWs (CCRW<sub>A</sub> or CCRW<sub>L</sub>) was the best model for more  
235 than 98% (53/54) of all movement paths and for at least 95% of the movement paths of  
236 each species (Table 3). For all species, the mean Akaike weight,  $w_{\text{CCRW}}$ , of paths with a  
237 CCRW as best model was > 0.94. According to the test of absolute fit, some of the  
238 movement paths best described by a CCRW were not different from it: 48% of caribou,  
239 25% of grizzlies, and 0% of polar bears (Table 3). While the TLW and CRW were never  
240 the best model of a movement path, the BW was the best model for one of the 22  
241 movement paths of the caribou. The mean Akaike weight of this BW was 0.42 and this  
242 path was different from the BW. For a visual representation of the fit of the models see  
243 Fig. 1 and for the results for each individual see Appendix S2.

244 For comparative purposes, we also present the results when the CCRW<sub>A</sub>, CCRW<sub>L</sub>, and  
245 CRW are excluded from the analysis and only the TLW and BW are considered as  
246 alternative hypotheses. Both the TLW and BW have a uniform probability density  
247 function to describe the turning angle frequency, and the same step length probability  
248 density functions as in Edwards *et al.* (2007). Thus comparing the  $AIC_c$  of these two  
249 models can be considered equivalent to current methods used by others to find evidence for

250 the Lévy walk. The TLW was better than the BW for 75% of the grizzly bears and 8% of  
251 polar bears (Table 4). The rest of the movement paths, including all caribou paths, were  
252 better described by the BW. While the BW was sufficient to explain the movement of half  
253 of the caribou and one grizzly bear, it was insufficient for all polar bears. All movement  
254 paths were different from the TLW according to the test of absolute fit.

255 Many of the parameter estimates for the CCRWs ( $CCRW_A$  or  $CCRW_L$ ) indicated that the  
256 movement paths could be divided into two distinct phases (Table 5). First, the mean step  
257 length of the intensive phase was shorter than that of the extensive phase for all species  
258 ( $\lambda_I > \lambda_E$ ; note that  $1/\lambda + a$  represents the mean). Second, the extensive phase for the grizzly  
259 and polar bears had more directed movement than the intensive phase ( $\kappa_E > 0$ ). However,  
260 we had weaker support for caribou, as the mean confidence interval for the scale parameter,  
261  $\kappa_E$ , overlapped with 0. A scale parameter,  $\kappa_E$ , of 0 reduces the von Mises distribution to  
262 the same circular uniform distribution used for the intensive phase. In addition, the  
263 caribou, the 15 grizzly bears with the  $CCRW_A$  as their best model, and the polar bears  
264 appeared to remain in the intensive phase for multiple steps. When modeled with the  
265  $CCRW_A$ , these animals had a greater than 50% chance of remaining in the intensive phase  
266 ( $\gamma_{II} > 0.5$ ). When modeled with the  $CCRW_L$ , they spent on average more than one step in  
267 the intensive phase ( $\alpha_I > 1$ ). However, we had weaker support for such behavioural  
268 persistence for the 5 grizzly bears with the  $CCRW_L$  as their best model because their mean  
269 number of steps in the intensive phase,  $\alpha_I$ , was only 0.28.

## 270 4 Discussion

271 We found substantial support for the two versions of the CCRW. 98% of the movement  
272 paths had one of these CCRWs as best model. Of these movement paths, 28% were

adequately described by the best CCRW version. In general, the estimated parameters from the CCRWs indicated that the movement patterns could be divided into two distinct movement behaviours, a directed extensive phase and a tortuous intensive phase consistent with an area-restricted search. However, not all movement paths were consistent with a CCRW. According to the test of absolute fit, the movement paths of many caribou, grizzly bears, and most polar bears were different from the best CCRW version, even though one of the CCRWs was, in almost all of these cases, the best model according to  $AIC_c$ . In addition, the confidence intervals on some parameter estimates indicated that the evidence for directed movement and behavioural persistence in the intensive phase was not strong for some species. These discrepancies indicate that although our versions of the CCRW can approximate the movement better than the three other models we investigated, it might be an incomplete representation of the search strategy used by some of the animals we studied.

We found no movement patterns consistent with the Lévy strategy, which is in line with recent studies suggesting that Lévy movement may be less common than originally thought (Edwards *et al.*, 2007, 2012; James, Plank & Edwards, 2011; Pyke, 2015, but see Humphries *et al.* 2012; Sims *et al.* 2012; Gautestad & Mysterud 2013). Although no movement paths had the TLW as its best model when all models were considered, support for TLW increased when the CCRWs were excluded from the set of alternative models. When the TLW was compared only to the BW, 75% of the grizzly bears and one polar bear had the TLW as their best model. This re-emphasizes the importance of comparing Lévy walk models to strong alternatives such as the CCRW (Auger-Méthé *et al.*, 2011; Jansen, Mashanova & Petrovskii, 2012; Plank, Auger-Méthé & Codling, 2013). It also supports the contention that some Lévy walk movement patterns might emerge from multiphasic movement or other mechanisms rather than providing evidence for the Lévy

297 search strategy per se (Benhamou, 2007; Plank & James, 2008; Breed, Severns & Edwards,  
298 2015; Reynolds, 2015). Finally, the fact that all empirical movement paths differed from  
299 the TLW further indicates that it was likely an inappropriate model for our data. This  
300 reiterates the importance of testing the absolute fit of a model (Auger-Méthé *et al.*, 2011;  
301 Plank, Auger-Méthé & Codling, 2013).

302 The fact that we found support for CCRWs is unsurprising given that there is ample  
303 evidence of species showing similar biphasic movement behaviour (e.g. Morales *et al.*, 2004;  
304 Jonsen, Myers & James, 2007; Dragon *et al.*, 2012), including caribou (Johnson *et al.*,  
305 2002a,b; Tyson, Wilson & Lane, 2011). However, our results contrast with previous  
306 research on semi-domesticated reindeer (*R. t. tarandus*), a Eurasian subspecies of caribou.  
307 We found that CCRWs and the two null models were better than the TLW for the winter  
308 movement of all caribou (Appendix S2). In contrast, previous studies found that the  
309 movement of reindeer in spring and early summer was more consistent with the Lévy walk  
310 than with null models (Mårell, Ball & Hofgaard, 2002; Edwards, 2011). These differences  
311 might be due to behavioural variation between subspecies or between wild and  
312 semi-domesticated animals. They may also result from differences in the sampling scale,  
313 habitat, and season examined in the studies. Mårell, Ball & Hofgaard (2002) showed that  
314 reindeer changed their movement strategies over the course of the summer. For caribou,  
315 Johnson *et al.* (2002a) showed stronger support for a two-behaviour model in winter than  
316 in summer and attributed the difference to increased patch heterogeneity due to snow  
317 conditions and lichen distributions. Thus, it is possible that caribou exhibit CCRW  
318 movement patterns in winter but not during the summer.

319 Unlike grizzlies and polar bears, one caribou had the BW as their best model. In addition,  
320 many caribou movement paths were not statistically different from the BW and the

321 parameter estimates indicated that the distinction between the two behaviours of CCRWs  
322 was not strong. Our caribou movement paths had the coarsest sampling scale and the  
323 smallest sample sizes (see Appendix S2). This sampling scheme may have favoured finding  
324 evidence for a simpler model in this species, and the small sample size might have  
325 contributed to the relatively low rate of rejection for caribou. However, Edwards (2011)  
326 also found that null models similar to the BW explained the movement of this species  
327 during part of the year, supporting our results that the BW is sufficient to explain the  
328 movement of some caribou. A single behaviour search strategy may be sufficient for large  
329 herbivores, which often rely on widely dispersed low-quality food rather than patches of  
330 highly nutritional items (Senft *et al.*, 1987).

331 CCRWs were the best model for all grizzlies and were sufficient to explain the movement  
332 paths of some individuals. We anticipated movement patterns consistent with a random  
333 search strategy because the bears in this population inhabit sparse and unpredictable  
334 environments and display home range drift (Edwards, Nagy & Derocher, 2009). Bears in  
335 this population vary in their foraging behaviours from a spectrum of near complete  
336 herbivory to carnivory (Edwards *et al.*, 2011). Such specialisation was related to changes in  
337 movement behaviours, with carnivores moving faster than herbivores (Edwards *et al.*,  
338 2011). Indeed, we would expect carnivores and herbivores to use different search strategies,  
339 and such individual variation might explain why the movement of only some individuals is  
340 adequately represented by CCRWs. We might expect the intensive movement associated  
341 with the area-restricted search to be more effective for the herbivorous bears exploiting  
342 immobile berry patches than for carnivores preying on vagile animals. Further research  
343 could investigate how differences in diet are reflected in the search strategies used by  
344 grizzlies.

345 CCRWs were the best model for all polar bears, but were insufficient to explain the  
346 movement paths of all individuals. The parameter estimates indicate that there is a strong  
347 differentiation in both step length and directional persistence between the behavioural  
348 phases, suggesting that there is evidence for two movement phases even though the  
349 movement is not adequately described by the CCRWs. Difference in these phases could be  
350 driven by a variety of factors, including alterations in movement according to sea ice  
351 condition. Since the movement behaviour of polar bears is associated with the high levels  
352 of sea ice drift they experience (Mauritzen *et al.*, 2003; Auger-Méthé, Lewis & Derocher,  
353 2016), neglecting sea ice drift may partially explain why our models were insufficient to  
354 explain their movement. Although studies have found movement consistent with random  
355 search strategies in animals experiencing drift from ocean and wind currents (e.g.,  
356 Fauchald & Tveraa, 2003; Humphries *et al.*, 2012; Sims *et al.*, 2012), neglecting currents  
357 can distort inference made from foraging movement models (Gaspar *et al.*, 2006). This  
358 distortion may be attributed to the difficulty of distinguishing between voluntary  
359 movement and drift, but it may also arise from the fact that many species use currents  
360 strategically when traveling (e.g., Weimerskirch *et al.*, 2000).

361 The test of absolute fit revealed that the models we explored failed to accurately represent  
362 72% of the movement paths. There are multiple potential reasons for the high rejection  
363 rate of this test, the first three of which are methodological in nature. First, animals are  
364 unlikely to move exactly as modelled by our idealised representation of search strategies,  
365 and with large sample sizes, any small deviation could result in rejection. While we  
366 explored two CCRW versions that differed in how we modeled the number of steps made in  
367 a movement phase, varying step length and turning angle distributions can further increase  
368 the absolute fit of the CCRWs (see Appendix S3). Second, although the models are good



369 representations of a movement path composed of biologically relevant steps, they are not  
370 necessarily good representations of observed movement. To estimate biologically relevant  
371 steps from sampled steps, we used the local turn method. Such procedures can distort  
372 movement paths and bias results in favour of Lévy walk models (Codling & Plank, 2011;  
373 Plank, Auger-Méthé & Codling, 2013). In particular, the test of absolute fit we used has a  
374 slightly inflated rejection rate when a  $10^\circ$  local turn threshold is used (Auger-Méthé *et al.*,  
375 2015). However, the method's ability to distinguish between the CCRW and TLW is robust  
376 to use of a  $10^\circ$  threshold (Auger-Méthé *et al.*, 2015), and we found consistent results over a  
377 range of threshold angles. The only noteworthy exceptions are that up to three grizzly bear  
378 movement paths had the TLW as best model when high threshold angles were used (e.g.  
379  $40^\circ$ ) and that when a threshold angle of  $50^\circ$  was used one grizzly bear movement path with  
380 a TLW as best model was not statistically different from it (see Appendix S1). Third,  
381 sampling scale can affect the observed movement pattern and thus behavioural inference  
382 (e.g., Codling & Hill, 2005; Andersen *et al.*, 2008; Plank & Codling, 2009). The data we  
383 used was sampled at a coarse temporal scale (daily for caribou or every 4hrs for bears).  
384 Thus, investigating movement paths with locations taken at a more frequent interval could  
385 potentially increase the absolute fit of CCRWs. However, we showed previously that, for  
386 polar bears, movement paths with locations taken every 30 min gave similar results: the  
387  $CCRW_A$  was better than the TLW, BW, and CRW, but was insufficient to explain the  
388 observed movement (Auger-Méthé *et al.*, 2015). Across sampling scales and species, we  
389 generally found stronger support for CCRWs compared to the BW and CRW, but in some  
390 cases these simpler models were favoured or had strong enough support to be kept as  
391 potential alternatives (see also Auger-Méthé *et al.*, 2015). In contrast, the stronger support  
392 for CCRWs over the TLW was constant across the three species studied and the three

393 different sampling scales (locations taken every 30 min, 4 hrs, 1 day), indicating that this  
394 finding is relatively robust to sampling scale.

395 In addition to these methodological reasons, there are at least four potential biological  
396 reasons for the lack of fit of these movement models. First, the Lévy walk and the  
397 area-restricted search strategy associated with CCRWs were developed for animals with  
398 scant knowledge of their environment (Knoppien & Reddingius, 1985;  
399 James, Plank & Edwards, 2011). Species like the caribou and polar bears exhibit some  
400 degree of site fidelity (Mauritzen, Derocher & Wiig, 2001; Faille *et al.*, 2010; Tracz *et al.*,  
401 2010), thus we can expect them to be at least moderately familiar with their environment.  
402 As many species display site fidelity and are capable of storing information on their  
403 habitat, there is increasing interest in memory-based movement models  
404 (Börger, Dalziel & Fryxell, 2008; Smouse *et al.*, 2010; Fagan *et al.*, 2013). Ignoring memory  
405 may distort analyses of random search strategies (Gautestad & Mysterud, 2013), and some  
406 memory-based search strategies have similar movement patterns to CCRWs with  
407 area-restricted search (e.g. Fronhofer, Hovestadt & Poethke, 2013). Thus, accounting for  
408 memory in movement analysis may help understand the search strategies used by animals  
409 with knowledge of their environment (e.g. Regular, Hedd & Montevecchi, 2013). Second,  
410 random search strategies were developed for animal searching outside of their perceptual  
411 range (Benhamou, 1992; James, Plank & Edwards, 2011). Many species have an acute  
412 sense of smell and are thought to use olfactory cues to find their prey (Conover, 2007).  
413 Such species include the grizzly and polar bear (Stirling, 1999; Conover, 2007), as well as  
414 species that have been suggested to follow a random search strategy (e.g., wandering  
415 albatross, *Diomedea exulans*, Nevitt, Losekoot & Weimerskirch, 2008; Humphries *et al.*,  
416 2012). As with knowledge of the environment, the use of sensory cues and the extent of the

417 perceptual range are likely to affect the type of search strategies used by animals  
418 (Nevitt, Losekoot & Weimerskirch, 2008; Fronhofer, Hovestadt & Poethke, 2013). Third,  
419 landscape features can alter animal movement patterns and affect their search strategy. In  
420 particular, ignoring resource density levels can distort analysis of random search strategies  
421 (Gautestad & Mysterud, 2013), and including landscape features in movement models can  
422 enhance our understanding of animals' foraging success (McKenzie *et al.*, 2012). Fourth,  
423 animals have an extensive behavioural repertoire and their movement paths often include  
424 behaviours other than searching for food. Neglecting to remove other behaviours is known  
425 to distort analysis of search strategies (Edwards *et al.*, 2007). We removed two types of  
426 resting periods, the denning period of bears and all steps where locations remained  
427 constant. In addition, we removed the main reproductive and mating periods of all species.  
428 However, given that our sampling interval was coarse and that the movement paths  
429 encompassed months, it is likely that many behaviours, including nursing, predator  
430 avoidance, and socialising, are still present in the movement paths. These four explanations  
431 for the lack of fit of simple movement models emphasises how difficult it is to understand  
432 how animals search for food, and echoes the calls for more mechanistic movement models  
433 (Nathan *et al.*, 2008; Schick *et al.*, 2008).

434 While we have movement patterns consistent with CCRWs and Brownian motion, there is  
435 likely no universal search strategy. Both species and individuals differ. Thus, we will only  
436 be able to accurately represent how animals search for food once we incorporate into  
437 movement models aspects such as memory, landscape features, and the effects of sampling  
438 on observed movement paths.

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457 #WL003104, #WL003122, #WL003282, #WL005352, #WL005375, #WL005598,  
458 UAAU#412305, #412405, #412505, #412605, #412705, #412805, #412905; Polar bears:  
459 GNWT #7376, UAAU #600904, UAAU #6001004, UAAU #600/03/12,)

## 460 **6 Data accessibility**

461 All time-series of step lengths and turning angles used in this manuscript are available from  
462 the University of Alberta Education & Research Archive:

463 For caribou: <https://era.library.ualberta.ca/files/bv405s9467#.V1sxSNcZ51Q>

464 For grizzly: <https://era.library.ualberta.ca/files/b4b29b605j#.V1sxl9cZ51Q>

465 For polar bear: <https://era.library.ualberta.ca/files/ms35tc50t#.V1sxt9cZ51Q>

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687 The following online Supporting Information is available for this article.

688 **Appendix S1** Variation in threshold angle

689 **Appendix S2** Model fit for each individual

690 **Appendix S3** Additional CCRW model

Table 1: Likelihood functions and number of parameters to estimate ( $k$ ) for the five models. For a description of the probability density functions:  $\psi_T(l)$ ,  $v_0(\theta)$ ,  $\phi(l)$ , and  $v(\theta)$ , see Table 2.

Model	Likelihood function	$k$
TLW	$\prod_{t=1}^n \psi_T(l_t   \mu_T, a, b) v_0(\theta_t)$	3
BW	$\prod_{t=1}^n \phi(l_t   \lambda, a) v_0(\theta_t)$	3
CRW	$\prod_{t=1}^n \phi(l_t   \lambda, a) v(\theta_t   \kappa)$	4
CCRW <sub>A</sub>	$\prod_{t=1}^n \Gamma_t \begin{pmatrix} \phi(l_t   \lambda_I, a) v_0(\theta_t) & 0 \\ 0 & \phi(l_t   \lambda_E, a) v(\theta_t   \kappa_E) \end{pmatrix} \begin{pmatrix} 1 \\ 1 \end{pmatrix}$ , $\Gamma_t = \begin{cases} (\delta_t, 1 - \delta_t) & \text{if } t = 1 \\ \begin{pmatrix} \gamma_{II} & 1 - \gamma_{II} \\ 1 - \gamma_{EE} & \gamma_{EE} \end{pmatrix} & \text{otherwise} \end{cases}$	7
CCRW <sub>L</sub>	$\prod_{t=1}^n \Gamma_t \begin{pmatrix} \phi(l_t   \lambda_I, a) v_0(\theta_t) & 0 \\ 0 & \phi(l_t   \lambda_E, a) v(\theta_t   \kappa_E) \end{pmatrix} \begin{pmatrix} 1 \\ 1 \end{pmatrix}$ , $\Gamma_t = \begin{cases} \boldsymbol{\delta}^\dagger & \text{if } t = 1 \\ \begin{pmatrix} 0 & 1 - \gamma_I(1) & \dots & 0 & \gamma_E(1) & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \dots & 1 - \gamma_I(m-1) & \gamma_E(m-1) & \dots & 0 \\ 0 & 0 & \dots & 1 - \gamma_I(m) & \gamma_E(m) & \dots & 0 \\ \gamma_E(1) & 0 & \dots & 0 & 1 - \gamma_E(1) & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots & \ddots & \vdots \\ \gamma_E(m-1) & 0 & \dots & 0 & 0 & \dots & 1 - \gamma_E(m-1) \\ \gamma_E(m) & 0 & \dots & 0 & 0 & \dots & 1 - \gamma_E(m) \end{pmatrix} & \text{otherwise} \end{cases}^\ddagger$	6

<sup>†</sup> As in Langrock *et al.* (2012), we are using the stationary distribution for the initial values,  $\boldsymbol{\delta}$ , of the Markov chain for CCRW<sub>L</sub>.

<sup>‡</sup> As in Langrock *et al.* (2012),  $\gamma_I(r) = \frac{p_I(r)}{(1 - \sum_{k=1}^{r-1} p_I(r))}$  and  $\gamma_E(r) = \frac{p_E(r)}{(1 - \sum_{k=1}^{r-1} p_E(r))}$ . For both phases, we are using a Poisson distribution,  $p_I(r)$  and  $p_E(r)$ , for the state dwell time. See Table 2 for a description of the Poisson distribution  $p(r)$ .



Table 2: Formulas for the probability density functions (PDFs) used in the models and the restrictions on their variables and parameters. The variables  $l$  and  $\theta$  represent step length and turning angle, respectively.

Distribution	Symbol	PDF	Restrictions
Exponential	$\phi(l \lambda, a)$	$\lambda e^{-\lambda(l-a)}$	$a \leq l, \lambda > 0$
Truncated Pareto	$\psi_{\Gamma}(l \mu_{\Gamma}, a, b)$	$\frac{(\mu_{\Gamma}-1)l^{-\mu_{\Gamma}}}{a^{1-\mu_{\Gamma}}-b^{1-\mu_{\Gamma}}}$	$a \leq l \leq b$ <sup>†</sup>
Von Mises	$v(\theta \kappa)$	$\frac{1}{\int_{-\pi}^{\pi} e^{\kappa \cos(\theta)} d\theta} e^{\kappa \cos(\theta)}$ <sup>‡,§</sup>	$\kappa > 0$
Uniform	$v_0(\theta)$	$\frac{1}{2\pi}$	
Poisson	$p(r \alpha)$	$\frac{\alpha^r}{r!} e^{-\alpha}$	$\alpha > 0$

<sup>†</sup> Unlike in Auger-Méthé *et al.* (2015), we are not placing restrictions on the estimated  $\mu_{\Gamma}$  values.

<sup>‡</sup> This is a simplified and expanded equation of the von Mises PDF. The same equation is often written with a modified Bessel function of the first kind and of order 0.

<sup>§</sup> These simplified versions assume that the distribution is centred at 0, for full version see Codling, Plank & Benhamou (2008).

Table 3: Relative and absolute fit of the five models on the movement paths of 22 caribou, 20 grizzlies, and 12 polar bears. For each model, we present the number of movement paths selected as best model with  $AIC_c$  and the mean Akaike weight,  $w$ , of these selected paths. Note that we used the summed Akaike weight of the  $CCRW_A$  and  $CCRW_L$  because these two models represent the movement pattern of the same search strategy. We also present how many of the selected paths are not different from the best model according to a test of absolute fit based on the step length distribution.

Model	N° as best model			$w$ of best model			N° p-value > 0.05		
	Caribou	Grizzly	Polar bear	Caribou	Grizzly	Polar bear	Caribou	Grizzly	Polar bear
$CCRW_A$	4	15	9	0.95	1.00	1.00	1	1	0
$CCRW_L$	17	5	3				9	4	0
TLW	0	0	0	–	–	–	–	–	–
BW	1	0	0	0.42	–	–	0	–	–
CRW	0	0	0	–	–	–	–	–	–

Table 4: Relative and absolute fit of the two models generally used in Lévy walk analysis. For each model, we present the number of movement paths selected as best model with  $AIC_c$  and the mean Akaike weight of these selected paths. We also present how many of the overall paths are not statistically different from the TLW and BW when only the step lengths are considered.

Model	N° as best model			$w$ of best model			N° p-value > 0.05		
	Caribou	Grizzly	Polar bear	Caribou	Grizzly	Polar bear	Caribou	Grizzly	Polar bear
TLW	0	15	1	–	1.00	1.00	0	0	0
BW	22	5	11	1.00	0.93	1.00	11	1	0

Table 5: Parameter estimates for the best models. The mean parameter estimates and associated confidence intervals (CIs) are presented for each species. Only the movement path of individuals that had the model as its best are used. The locations of caribou were taken daily, those of grizzly and polar bears were taken every 4 hrs.

Symbol (unit)	Description	Caribou	Grizzly	Polar bear
$a$ ( $km$ )	Minimum step length of the BW, CCRW <sub>A</sub> , and CCRW <sub>L</sub>	0.053	0.0030	0.023
$\gamma_{II}$	Probability of remaining in the CCRW <sub>A</sub> 's intensive phase	1.00 (0.98-1.00)	0.54 (0.44-0.64)	0.83 (0.78-0.88)
$\gamma_{EE}$	Probability of remaining in the CCRW <sub>A</sub> 's extensive phase	0.97 (0.89-1.00)	0.85 (0.80-0.90)	0.96 (0.96-0.97)
$\kappa_E$	Scale parameter of the directional correlation of the CCRWs' extensive phase	0.22 (0.00-1.14)	0.41 (0.22-0.62)	1.1 (1.0-1.3)
$\lambda$ ( $km^{-1}$ )	Rate parameter of the exponential distribution of the BW	0.43 (0.36-0.50)	—	—
$\lambda_I$ ( $km^{-1}$ )	Rate parameter of the CCRWs' intensive phase	7.7 (1.2-18.1)	53 (35-82)	16 (13-21)
$\lambda_E$ ( $km^{-1}$ )	Rate parameter of the CCRWs' extensive phase	0.37 (0.25-0.54)	0.56 (0.49-0.63)	0.19 (0.18-0.21)
$\alpha_I$	Mean of the Poisson for CCRW <sub>L</sub> 's intensive phase	15 (10-19)	0.28 (0.13-0.53)	13 (9-16)
$\alpha_E$	Mean of the Poisson for CCRW <sub>L</sub> 's extensive phase	14 (9-19)	4.0 (3.3-5.2)	17 (15-19)

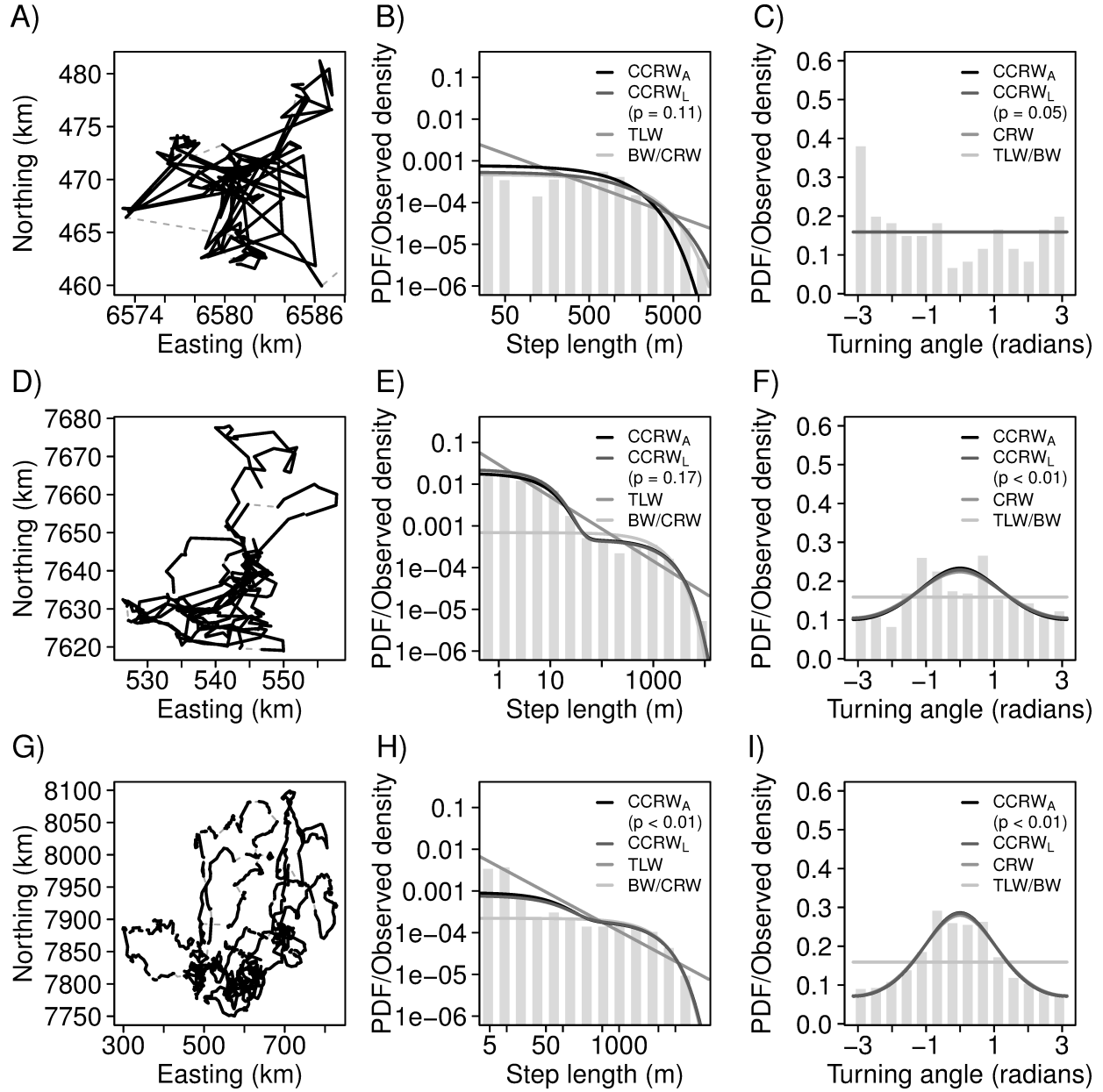


Figure 1: Fit of the models on the movement path of each species: (A-C) caribou, (D-F) grizzly, and (G-I) polar bear. (A, D, G) black lines represent the movement path using the  $10^\circ$  threshold angle and the gray dashed line the missing data. (B, E, H) Step length frequency with the probability density function (PDF) of each model, on log-log axes. (C, F, I) Turning angle frequency with the PDF of each model. The best model for these three individuals was either the  $CCRW_A$  or  $CCRW_L$  with Akaike weight:  $w_{CCRW} > 0.99$ . The p-value of the test of absolute fit for the step length and turning angle distributions of the best model are indicated in the legend. See Appendix S2 for the other individuals.