Evaluating random search strategies in three mammals from distinct feeding guilds

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Summary

1. Searching allows animals to find food, mates, shelter, and other resources essential for survival and reproduction, and is thus among the most important activities performed by animals. Theory predicts that animals will use random search strategies in highly variable and unpredictable environments. Two prominent models have been suggested for animals searching in sparse and heterogeneous environments: (i) the Lévy walk and (ii) the composite correlated random walk (CCRW) and its associated area-restricted search behaviour. Until recently, it was difficult to differentiate between the movement patterns of these two strategies.

2. Using a new method that assesses whether movement patterns are consistent with these two strategies and two other common random search strategies, we investigated the movement behaviour of three species inhabiting sparse northern environments: woodland caribou (*Rangifer tarandus caribou*), barren ground grizzly bear (*Ursus arctos*), and polar bear (*U. maritimus*). These three species vary widely in their diets, and thus allow us to contrast the movement patterns of animals from different feeding guilds.

3. Our results showed that, although more traditional methods would have found evidence for the Lévy walk for some individuals, a comparison of the Lévy walk to CCRWs showed stronger support for the latter. While a CCRW was the best model for most individuals, there was a range of support for its absolute fit. A CCRW was sufficient to explain the movement of nearly half of herbivorous caribou and a quarter of omnivorous grizzly bears, but was insufficient to explain the movement of all carnivorous polar bears.

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

Keywords

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

1 Introduction

Searching is among an animal's most important activities as it provides the means to find food, mates, shelter, and other resources essential for survival and reproduction (Bell, 1991). Search efficiency will affect performance and fitness, and thus we expect animals to use movement strategies that minimise the costs of locating resources (Zollner & Lima, 1999; Conradt *et al.*, 2003). The importance of this behaviour has driven ecologists to focus on animals' search strategies (e.g., Bell, 1991; Benhamou, 1994; Viswanathan *et al.*, 1999), and the recent increase in the availability of movement data has allowed this field to flourish (e.g., Fauchald & Tveraa, 2003; Nevitt, Losekoot & Weimerskirch, 2008; Humphries *et al.*, 2010). One focus has been to assess whether animals use the search strategies that theory predicts will be optimal in their environments (e.g., Humphries *et al.*, 2010; Sims *et al.*, 2012). Using movement data for this assessment remains challenging because the efficiency of search strategies changes over environmental gradients and the movement patterns they produce can be difficult to differentiate (Zollner & Lima, 1999; Bartumeus *et al.*, 2002; Benhamou, 2007; Plank & Codling, 2009). The efficacy of movement strategies are dependent on the variability and predictability of resource distributions. When resources are unpredictable in space and time, random search strategies are expected to emerge (Mueller & Fagan, 2008). Although animals are known to use perceptual cues to detect nearby resources, empiricists have found support for the use of random search strategies (e.g., Humphries *et al.*, 2010; Sims *et al.*, 2012). Theorists have proposed a set of random search strategies that are thought to be optimal under different conditions. While simple Brownian motion may be sufficient in productive areas, the Lévy walk may be advantageous in sparse environments because its rare, extremely long steps enable animals to explore new areas (Bartumeus *et al.*, 2002; Humphries *et al.*, 2010, but see James, Plank & Edwards 2011; Benhamou & Collet 2015; Pyke 2015). Relative to Brownian motion, the Lévy walk is increasingly efficient with decreasing food density (Viswanathan *et al.*, 1999; Bartumeus *et al.*, 2002). When food density is low, the Lévy walk is also more efficient than a correlated random walk (Bartumeus *et al.*, 2005). The correlated random walk is a search strategy characterised by nearly straight movement that was shown to be efficient at finding sparsely distributed patches (Zollner & Lima, 1999). The composite correlated random walk (CCRW) is a two-behaviour strategy that is more efficient than single-behaviour models in heterogeneous landscapes (Knoppien & Reddingius, 1985; Benhamou, 1992; Plank & James, 2008; Benhamou & Collet, 2015). The 'extensive' phase of the CCRW uses the nearly straight movement that makes the correlated random walk efficient at finding patches. The discovery of a food item triggers the 'intensive' phase, which is characterised by slower, more tortuous movement and sometimes referred as area-restricted search. These two behavioural phases allow animals to adjust their movement according to local food density and the intensive phase enables them to stay within patches, even when patches have no perceptible boundaries (Knoppien & Reddingius, 1985; Benhamou, 1992). Many environments are sparse, heterogeneous, and unpredictable. While Brownian motion and correlated random walk might be insufficient in these instances, both the Lévy and CCRW may be advantageous random search strategies.

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

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

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

Our third species, the polar bear (*U. maritimus*), is a specialised marine carnivore. Polar bears, like many other predators that have been the focus of search strategy studies, exploit the unpredictable marine environment (e.g., Humphries *et al.*, 2010, 2012, but see Regular, Hedd & Montevecchi 2013). Polar bears exhibit site fidelity (Mauritzen, Derocher & Wiig, 2001), which could encourage the use of memory-based search strategies. However, other species that exhibit site fidelity are also thought to use random search strategies or a mixture of memory and random search strategies (e.g., Humphries *et al.*, 2012; Gautestad & Mysterud, 2013). Polar bears use the sea ice as a platform to hunt seals (Stirling & Derocher, 2012). Sea ice extent changes seasonally and local ice concentration can vary drastically over short time scales (Maslanik & Barry, 1989; Johannessen *et al.*, 2004), which may make random search strategies advantageous.

Using data collected when these three species were expected to be searching for food, we investigated whether their movement patterns were consistent with one of these four random search strategies. To do so, we compared the relative fit of a set of models, each representing the movement pattern of one of the search strategies. We then assessed the absolute fit of the best model to verify whether it described the observed movement well.

2 Materials and methods

2.1 Modeling search strategies

We used the method described in Auger-Méthé *et al.* (2015) to assess whether the movement patterns of three species were consistent with a set of search strategies. This method defines likelihood functions that model the movement pattern of each of the four search strategies (Table 1), and can be considered a generalised and statistically rigorous extension of earlier methods. Each likelihood function was applied to the time series of step lengths, l_t, and turning angles, θ_t, of each individual. The movement pattern of Lévy strategy was represented by a truncated Lévy walk (TLW), which used a truncated Pareto distribution for the step length, $\psi_{\mathrm{T}}(l)$, and a circular uniform distribution for the turning angle, $v_0(\theta)$ (Table 2). The movement pattern of the Brownian motion was represented by a Brownian walk (BW), which used an exponential distribution for the step length, $\phi_{\mathrm{T}}(l)$, and a circular uniform distribution for the turning angle, $v_0(\theta)$ (Table 2). The correlated random walk (CRW) also used an exponential distribution for the step length, $\phi_{\mathrm{T}}(l)$, but in combination with a von Mises distribution centred at 0 for the turning angle, $v(\theta)$ (Table 2). The CCRW version from Auger-Méthé *et al.* (2015), which we refer to as $\mathrm{CCRW}_{\mathrm{A}}$, used a hidden Markov model with two movement behaviours (Table 1). The movement pattern of the intensive phase was represented by a Brownian walk with exponential distribution for the step length, $\phi(l)$, and a circular uniform distribution for the turning angle, $v_0(\theta)$ (Table 2). The movement pattern of the extensive phase was represented by a correlated random walk with an exponential distribution for the step length, $\phi(l)$, and a von Mises distribution centred at 0 for the turning angle, $v(\theta)$ (Table 2). As we suggested in

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

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

2.2 Description of movement data

We used the movement data of three northern mammal species (data available on the University of Alberta Education & Research Archive: `https://era.library.ualberta.ca/`). To capture rare events, such as the long steps characteristic of the Lévy walk, we attempted to get time series representing close to a year of movement behaviour. However, we also tried to limit the time series to movement performed while searching. As detailed below, we removed all sections of the datasets known to be associated with reproduction and resting, as the changes in movement patterns associated with such behaviours could affect our analyses (e.g., DeMars *et al.*, 2013). We also started each time series a minimum of two weeks after the collaring event because capturing procedures associated with collaring affect the movement of some species (e.g., Morellet *et al.*, 2009; Thiemann *et al.*, 2013). The time series of some individuals were further reduced by missing observations and collar failures.

The first dataset included the movement paths of 22 female caribou from the boreal plains region of northeastern British Columbia, Canada. These females were captured during February and March 2011 and fitted with G2110E collars from Advanced Telemetry Systems Inc. (Isanti, MN, USA). The collars provided daily Global Positioning System (GPS) locations. We removed the calving and rut periods, as well as the two weeks post collaring, by limiting the time series to locations collected between November 1st 2011 to April 30th 2012 (Ferguson & Elkie, 2004). The second dataset included the movement paths of 20 grizzly bears from the Mackenzie Delta, Northwest Territories, Canada. These bears were collared in May and June (close to den emergence) 2003-2009. For each individual, we used locations collected during the first year after collaring, in the period between July 1st to November 30th (or den entrance). Starting July 1st excluded the peak of the mating season (MacHutchon, 1996) and the two weeks following the collaring events. The third dataset included the movement paths of 12 polar bears from the Beaufort Sea. These bears were collared in April and May 2008-2010. To exclude the two weeks after collaring, we started the time series June 1st. We used locations collected until the subsequent June 1st. As some pregnant females of the Beaufort Sea give birth in dens on the moving sea ice (Amstrup & Gardner, 1994), it is difficult to identify den location. To exclude denning individuals, we included only juveniles and females accompanied with cubs-of-the-year or yearlings when collared. Restricting the analysis to these individuals also removed the potential for mating events in the time series. The locations of both the grizzly and polar bears are GPS locations taken every 4hrs with Gen II-IV collars from Telonics Inc. (Mesa, AZ, USA).

The collars of all of these animals were programmed to collect locations at regular time intervals. Transforming sampled steps into biologically relevant steps is among the most difficult challenges of using GPS data in ecology (Hebblewhite & Haydon, 2010), and various methods have been proposed (e.g., Codling & Plank, 2011). We chose to use the local turn method, a technique that creates one step out of all consecutive sampled steps with a turning angle smaller than a threshold angle (see Codling & Plank, 2011; Auger-Méthé *et al.*, 2015). This technique, as well as other similar methods, can cause the misidentification of CCRWs for Lévy walks (Codling & Plank, 2011; Plank, Auger-Méthé & Codling, 2013). However, misidentifications are more likely to occur when high threshold angles are used (Codling & Plank, 2011; Plank, Auger-Méthé & Codling, 2013). We chose a threshold angle of 10° because this small value limited the potential for misidentification and interpreted movement in the same general direction (i.e., any sampled step within the 20° forward sector) as part of a biologically relevant step (Auger-Méthé *et al.*, 2015). To verify that variations in threshold angles did not affect the results, we also explored a range of threshold angles. We show in Appendix S1 that the results were broadly similar regardless of the threshold angle used. Note that this local turn method can impact the test of absolute fit based on turning angle distribution (Auger-Méthé *et al.*, 2015), and we presented only the test of absolute fit for the step length distribution. Because missing locations can affect steps defined by the local turn method, we included only individuals that had a time series with $< 30\%$ of the locations missing. We also limited the time series to those with a minimum of 50 steps (Appendix S2 presents the range of sample size). We applied the models to the data from each individual separately.

3 Results

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

For comparative purposes, we also present the results when the CCRW$_{\text{A}}$, CCRW$_{\text{L}}$, and CRW are excluded from the analysis and only the TLW and BW are considered as alternative hypotheses. Both the TLW and BW have a uniform probability density function to describe the turning angle frequency, and the same step length probability density functions as in Edwards *et al.* (2007). Thus comparing the AIC_c of these two models can be considered equivalent to current methods used by others to find evidence for the Lévy walk. The TLW was better than the BW for 75% of the grizzly bears and 8% of polar bears (Table 4). The rest of the movement paths, including all caribou paths, were better described by the BW. While the BW was sufficient to explain the movement of half of the caribou and one grizzly bear, it was insufficient for all polar bears. All movement paths were different from the TLW according to the test of absolute fit.

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

4 Discussion

We found substantial support for the two versions of the CCRW. 98% of the movement 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 search strategy per se (Benhamou, 2007; Plank & James, 2008; Breed, Severns & Edwards, 2015; Reynolds, 2015). Finally, the fact that all empirical movement paths differed from the TLW further indicates that it was likely an inappropriate model for our data. This reiterates the importance of testing the absolute fit of a model (Auger-Méthé *et al.*, 2011; Plank, Auger-Méthé & Codling, 2013).

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

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

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

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

The test of absolute fit revealed that the models we explored failed to accurately represent 72% of the movement paths. There are multiple potential reasons for the high rejection rate of this test, the first three of which are methodological in nature. First, animals are unlikely to move exactly as modelled by our idealised representation of search strategies, and with large sample sizes, any small deviation could result in rejection. While we explored two CCRW versions that differed in how we modeled the number of steps made in a movement phase, varying step length and turning angle distributions can further increase the absolute fit of the CCRWs (see Appendix S3). Second, although the models are good representations of a movement path composed of biologically relevant steps, they are not necessarily good representations of observed movement. To estimate biologically relevant steps from sampled steps, we used the local turn method. Such procedures can distort movement paths and bias results in favour of Lévy walk models (Codling & Plank, 2011; Plank, Auger-Méthé & Codling, 2013). In particular, the test of absolute fit we used has a slightly inflated rejection rate when a 10° local turn threshold is used (Auger-Méthé *et al.*, 2015). However, the method's ability to distinguish between the CCRW and TLW is robust to use of a 10° threshold (Auger-Méthé *et al.*, 2015), and we found consistent results over a range of threshold angles. The only noteworthy exceptions are that up to three grizzly bear movement paths had the TLW as best model when high threshold angles were used (e.g. 40°) and that when a threshold angle of 50° was used one grizzly bear movement path with a TLW as best model was not statistically different from it (see Appendix S1). Third, sampling scale can affect the observed movement pattern and thus behavioural inference (e.g., Codling & Hill, 2005; Andersen *et al.*, 2008; Plank & Codling, 2009). The data we used was sampled at a coarse temporal scale (daily for caribou or every 4hrs for bears). Thus, investigating movement paths with locations taken at a more frequent interval could potentially increase the absolute fit of CCRWs. However, we showed previously that, for polar bears, movement paths with locations taken every 30 min gave similar results: the $\mathrm{CCRW}_{\mathrm{A}}$ was better than the TLW, BW, and CRW, but was insufficient to explain the observed movement (Auger-Méthé *et al.*, 2015). Across sampling scales and species, we generally found stronger support for CCRWs compared to the BW and CRW, but in some cases these simpler models were favoured or had strong enough support to be kept as potential alternatives (see also Auger-Méthé *et al.*, 2015). In contrast, the stronger support for CCRWs over the TLW was constant across the three species studied and the three different sampling scales (locations taken every 30 min, 4 hrs, 1 day), indicating that this finding is relatively robust to sampling scale.

In addition to these methodological reasons, there are at least four potential biological reasons for the lack of fit of these movement models. First, the Lévy walk and the area-restricted search strategy associated with CCRWs were developed for animals with scant knowledge of their environment (Knoppien & Reddingius, 1985; James, Plank & Edwards, 2011). Species like the caribou and polar bears exhibit some degree of site fidelity (Mauritzen, Derocher & Wiig, 2001; Faille *et al.*, 2010; Tracz *et al.*, 2010), thus we can expect them to be at least moderately familiar with their environment. As many species display site fidelity and are capable of storing information on their habitat, there is increasing interest in memory-based movement models (Börger, Dalziel & Fryxell, 2008; Smouse *et al.*, 2010; Fagan *et al.*, 2013). Ignoring memory may distort analyses of random search strategies (Gautestad & Mysterud, 2013), and some memory-based search strategies have similar movement patterns to CCRWs with area-restricted search (e.g. Fronhofer, Hovestadt & Poethke, 2013). Thus, accounting for memory in movement analysis may help understand the search strategies used by animals with knowledge of their environment (e.g. Regular, Hedd & Montevecchi, 2013). Second, random search strategies were developed for animal searching outside of their perceptual range (Benhamou, 1992; James, Plank & Edwards, 2011). Many species have an acute sense of smell and are thought to use olfactory cues to find their prey (Conover, 2007). Such species include the grizzly and polar bear (Stirling, 1999; Conover, 2007), as well as species that have been suggested to follow a random search strategy (e.g., wandering albatross, *Diomedea exulans*, Nevitt, Losekoot & Weimerskirch, 2008; Humphries *et al.*, 2012). As with knowledge of the environment, the use of sensory cues and the extent of the perceptual range are likely to affect the type of search strategies used by animals (Nevitt, Losekoot & Weimerskirch, 2008; Fronhofer, Hovestadt & Poethke, 2013). Third, landscape features can alter animal movement patterns and affect their search strategy. In particular, ignoring resource density levels can distort analysis of random search strategies (Gautestad & Mysterud, 2013), and including landscape features in movement models can enhance our understanding of animals' foraging success (McKenzie *et al.*, 2012). Fourth, animals have an extensive behavioural repertoire and their movement paths often include behaviours other than searching for food. Neglecting to remove other behaviours is known to distort analysis of search strategies (Edwards *et al.*, 2007). We removed two types of resting periods, the denning period of bears and all steps where locations remained constant. In addition, we removed the main reproductive and mating periods of all species. However, given that our sampling interval was coarse and that the movement paths encompassed months, it is likely that many behaviours, including nursing, predator avoidance, and socialising, are still present in the movement paths. These four explanations for the lack of fit of simple movement models emphasises how difficult it is to understand how animals search for food, and echoes the calls for more mechanistic movement models (Nathan *et al.*, 2008; Schick *et al.*, 2008).

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

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6 Data accessibility

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

For caribou: `https://era.library.ualberta.ca/files/bv405s9467#.V1sxSNcZ5lQ`

For grizzly: `https://era.library.ualberta.ca/files/b4b29b605j#.V1sxl9cZ5lQ`

For polar bear: `https://era.library.ualberta.ca/files/ms35tc50t#.V1sxt9cZ5lQ`

Literature Cited

Adamczewski, J.Z., Gates, C.C., Hudson, R.J. & Price, M.A. (1987) Seasonal changes in body composition of mature female caribou and calves (*Rangifer tarandus groenlandicus*) on an arctic island with limited winter resources. *Canadian Journal of Zoology*, **65**, 1149–1157.

Amstrup, S.C. & Gardner, C. (1994) Polar bear maternity denning in the Beaufort Sea. *Journal of Wildlife Management*, **58**, 1–10.

Andersen, M., Derocher, A.E., Wiig, Ø. & Aars, J. (2008) Movements of two Svalbard polar bears recorded using geographical positioning system satellite transmitters. *Polar Biology*, **31**, 905–911.

Auger-Méthé, M., Clair, C.C.S., Lewis, M.A. & Derocher, A.E. (2011) Sampling rate and misidentification of Lévy and non-Lévy movement paths: comment. *Ecology*, **92**, 1699–1701.

Auger-Méthé, M., Plank, M.J. & Codling, E.A. (2014) Distinguishing between Lévy walks and strong alternative models: Comment. *Ecology*, **95**, 1104–1109.

Auger-Méthé, M., Derocher, A.E., Plank, M.J., Codling, E.A. & Lewis, M.A. (2015) Differentiating the Lévy from a composite correlation random walk. *Methods in Ecology and Evolution*, **6**, 1179–1189.

Auger-Méthé, M., Lewis, M.A. & Derocher, A.E. (2016) Home ranges in moving habitats: polar bears and sea ice. *Ecography*, **39**, 26–35.

Bartumeus, F., Catalan, J., Fulco, U.L., Lyra, M.L. & Viswanathan, G.M. (2002) Optimizing the encounter rate in biological interactions: Lévy versus Brownian strategies. *Physical Review Letters*, **88**, 097901.

Bartumeus, F., Luz, M.G.E.D., Viswanathan, G.M. & Catalan, J. (2005) Animal search strategies: a quantitative random-walk analysis. *Ecology*, **86**, 3078–3087.

Bell, W.J. (1991) *Searching behaviour: the behavioural ecology of finding resources.* Chapman and Hall Ltd.

Benhamou, S. (1992) Efficiency of area-concentrated searching behaviour in a continuous patchy environment. *Journal of Theoretical Biology*, **159**, 67–81.

Benhamou, S. (1994) Spatial memory and searching efficiency. *Animal Behaviour*, **47**, 1423–1433.

Benhamou, S. (2007) How many animals really do the Lévy walk? *Ecology*, **88**, 1962–1969.

Benhamou, S. & Collet, J. (2015) Ultimate failure of the Lévy foraging hypothesis: two-scale searching strategies outperform scale-free ones even when prey are scarce and cryptic. *Journal of Theoretical Biology*, **387**, 221–227.

Bolker, B.M. (2008) *Ecological models and data in R.* Princeton University Press, Princeton, USA.

Börger, L., Dalziel, B.D. & Fryxell, J.M. (2008) Are there general mechanisms of animal home range behaviour? A review and prospects for future research. *Ecology Letters*, **11**, 637–650.

Breed, G.A., Severns, P.M. & Edwards, A.M. (2015) Apparent power-law distributions in animal movements can arise from intraspecific interactions. *Journal of The Royal Society Interface*, **12**, 20140927.

Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference: a practical information-theoretic approach 2nd Ed.* Springer, New York, USA.

Codling, E.A. & Hill, N.A. (2005) Sampling rate effects on measurements of correlated and biased random walks. *Journal of Theoretical Biology*, **233**, 573–588.

Codling, E.A. & Plank, M.J. (2011) Turn designation, sampling rate and the misidentification of power laws in movement path data using maximum likelihood estimates. *Theoretical Ecology*, **4**, 397–406.

Codling, E.A., Plank, M.J. & Benhamou, S. (2008) Random walk models in biology. *Journal of the Royal Society Interface*, **5**, 813–834.

Conover, M.R. (2007) *Predator-prey dynamics: the role of olfaction.* CRC Press, Boca Raton, USA.

Conradt, L., Zollner, P.A., Roper, T.J., Frank, K. & Thomas, C.D. (2003) Foray search: an effective systematic dispersal strategy in fragmented landscapes. *The American Naturalist*, **161**, 905–915.

DeMars, C.A., Auger-Méthé, M., Schlägel, U.E. & Boutin, S. (2013) Inferring parturition and neonate survival from movement patterns of female ungulates: a case study using woodland caribou. *Ecology and Evolution*, **3**, 4149–4160.

Dragon, A.C., Bar-Hen, A., Monestiez, P. & Guinet, C. (2012) Comparative analysis of methods for inferring successful foraging areas from Argos and GPS tracking data. *Marine Ecology Progress Series*, **452**, 253–267.

Edwards, A.M. (2011) Overturning conclusions of Lévy flight movement patterns by fishing boats and foraging animals. *Ecology*, **92**, 1247–1257.

Edwards, A.M., Freeman, M.P., Breed, G.A. & Jonsen, I.D. (2012) Incorrect Likelihood Methods Were Used to Infer Scaling Laws of Marine Predator Search Behaviour. *PLoS ONE*, **7**, e45174.

Edwards, A.M., Phillips, R.A., Watkins, N.W., Freeman, M.P., Murphy, E.J., Afanasyev, V., Buldyrev, S.V., da Luz, M.G.E., Raposo, E.P. & Stanley, H.E. (2007) Revisiting Lévy flight search patterns of wandering albatrosses, bumblebees and deer. *Nature*, **449**, 1044–1048.

Edwards, M.A., Derocher, A.E., Hobson, K.A., Branigan, M. & Nagy, J.A. (2011) Fast carnivores and slow herbivores: differential foraging strategies among grizzly bears in the Canadian Arctic. *Oecologia*, **165**, 877–889.

Edwards, M.A., Nagy, J.A. & Derocher, A.E. (2009) Low site fidelity and home range drift in a wide-ranging, large Arctic omnivore. *Animal Behaviour*, **77**, 23–28.

Fagan, W.F., Lewis, M.A., Auger-Méthé, M., Avgar, T., Benhamou, S., Breed, G., LaDage, L., Schlägel, U.E., Tang, W., Papastamatiou, Y.P., Forester, J. & Mueller, T. (2013) Spatial memory and animal movement. *Ecology Letters*, **16**, 1316–1329.

Faille, G., Dussault, C., Ouellet, J.P., Fortin, D., Courtois, R., St-Laurent, M.H. & Dussault, C. (2010) Range fidelity: The missing link between caribou decline and habitat alteration? *Biological Conservation*, **143**, 2840–2850.

Fauchald, P. & Tveraa, T. (2003) Using first-passage time in the analysis of area-restricted search and habitat selection. *Ecology*, **84**, 282–288.

Ferguson, S. & Elkie, P. (2004) Seasonal movement patterns of woodland caribou (*Rangifer tarandus caribou*). *Journal of Zoology*, **262**, 125–134.

Fronhofer, E.A., Hovestadt, T. & Poethke, H.J. (2013) From random walks to informed movement. *Oikos*, **122**, 857–866.

Gaspar, P., Georges, J.Y., Fossette, S., Lenoble, A., Ferraroli, S. & Maho, Y.L. (2006) Marine animal behaviour: neglecting ocean currents can lead us up the wrong track. *Proceedings of the Royal Society B*, **273**, 2697–2702.

Gautestad, A.O. & Mysterud, A. (2013) The Lévy flight foraging hypothesis: forgetting about memory may lead to false verification of Brownian motion. *Movement Ecology*, **1**, 9.

Hebblewhite, M. & Haydon, D.T. (2010) Distinguishing technology from biology: a critical review of the use of GPS telemetry data in ecology. *Philosophical Transactions of the Royal Society B*, **365**, 2303–2312.

Hilderbrand, G.V., Schwartz, C.C., Robbins, C.T., Jacoby, M.E., Hanley, T.A., Arthur, S.M. & Servheen, C. (1999) The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. *Canadian Journal of Zoology*, **77**, 132–138.

Humphries, N.E., Queiroz, N., Dyer, J.R.M., Pade, N.G., Musyl, M.K., Schaefer, K.M., Fuller, D.W., Brunnschweiler, J.M., Doyle, T.K. & Houghton, J.D.R. (2010) Environmental context explains Lévy and Brownian movement patterns of marine predators. *Nature*, **465**, 1066–1069.

Humphries, N.E., Weimerskirch, H., Queiroz, N., Southall, E.J. & Sims, D.W. (2012) Foraging success of biological Lévy flights recorded in situ. *Proceedings of the National Academy of Sciences*, **109**, 7169–7174.

James, A., Plank, M.J. & Edwards, A.M. (2011) Assessing Lévy walks as models of animal foraging. *Journal of the Royal Society Interface*, **8**, 1233–1247.

Jansen, V.A.A., Mashanova, A. & Petrovskii, S. (2012) Comment on Lévy Walks Evolve Through Interaction Between Movement and Environmental Complexity. *Science*, **335**, 918–918.

Johannessen, O.M., Bengtsson, L., Miles, M.W., Kuzmina, S.I., Semenov, V.A., Alekseev, G.V., Nagurnyi, A.P., Zakharov, V.F., Bobylev, L.P. & Pettersson, L.H. (2004) Arctic climate change: Observed and modelled temperature and sea-ice variability. *Tellus A*, **56**, 328–341.

Johnson, C.J., Parker, K.L., Heard, D.C. & Gillingham, M.P. (2002a) Movement parameters of ungulates and scale-specific responses to the environment. *Journal of Animal Ecology*, **71**, 225–235.

Johnson, C.J., Parker, K.L., Heard, D.C. & Gillingham, M.P. (2002b) A multiscale behavioral approach to understanding the movements of woodland caribou. *Ecological Applications*, **12**, 1840–1860.

Jonsen, I.D., Myers, R.A. & James, M.C. (2007) Identifying leatherback turtle foraging behaviour from satellite telemetry using a switching state-space model. *Marine Ecology Progress Series*, **337**, 255–264.

Knoppien, P. & Reddingius, J. (1985) Predators with two modes of searching: a mathematical model. *Journal of Theoretical Biology*, **114**, 273–301.

Langrock, R., King, R., Matthiopoulos, J., Thomas, L., Fortin, D. & Morales, J.M. (2012) Flexible and practical modeling of animal telemetry data: hidden Markov models and extensions. *Ecology*, **93**, 2336–2342.

MacHutchon, A. (1996) Grizzly bear habitat use study, Ivvavik National Park, Yukon. *Final Report. Western Arctic District, Parks Canada, Inuvik, Canada*, pp. xii+142.

Mårell, A., Ball, J.P. & Hofgaard, A. (2002) Foraging and movement paths of female reindeer: insights from fractal analysis, correlated random walks, and Lévy flights. *Canadian Journal of Zoology*, **80**, 854–865.

Maslanik, J.A. & Barry, R.G. (1989) Short-term interactions between atmospheric synoptic conditions and sea-ice behaviour in the Arctic. *Annals of Glaciology*, **12**, 113–117.

Mauritzen, M., Derocher, A.E., Pavlova, O. & Wiig, Ø. (2003) Female polar bears, *Ursus maritimus*, on the Barents Sea drift ice: walking the treadmill. *Animal Behaviour*, **66**, 107–113.

Mauritzen, M., Derocher, A.E. & Wiig, Ø. (2001) Space-use strategies of female polar bears in a dynamic sea ice habitat. *Canadian Journal of Zoology*, **79**, 1704–1713.

McKenzie, H.W., Merrill, E.H., Spiteri, R.J. & Lewis, M.A. (2012) How linear features alter predator movement and the functional response. *Interface Focus*, **2**, 205–216.

McLoughlin, P.D., Case, R.L., Gau, R.J., Ferguson, S.H. & Messier, F. (1999) Annual and seasonal movement patterns of barren-ground grizzly bears in the central Northwest Territories. *Ursus*, **11**, 79–86.

Morales, J.M., Haydon, D.T., Frair, J., Holsinger, K.E. & Fryxell, J.M. (2004) Extracting more out of relocation data: building movement models as mixtures of random walks. *Ecology*, **85**, 2436–2445.

Morellet, N., Verheyden, H., Angibault, J.M., Cargnelutti, B., Lourtet, B. & Hewison, M.A.J. (2009) The effect of capture on ranging behaviour and activity of the European roe deer *Capreolus capreolus*. *Wildlife Biology*, **15**, 278–287.

Mueller, T. & Fagan, W.F. (2008) Search and navigation in dynamic environments - from individual behaviors to population distributions. *Oikos*, **117**, 654–664.

Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D. & Smouse, P.E. (2008) A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences*, **105**, 19052–19059.

Nevitt, G.A., Losekoot, M. & Weimerskirch, H. (2008) Evidence for olfactory search in wandering albatross, *Diomedea exulans*. *Proceedings of the National Academy of Sciences*, **105**, 4576–4581.

Parker, K.L., Barboza, P.S. & Stephenson, T.R. (2005) Protein conservation in female caribou (*Rangifer tarandus*): effects of decreasing diet quality during winter. *Journal of Mammalogy*, **86**, 610–622.

Plank, M.J., Auger-Méthé, M. & Codling, E.A. (2013) Lévy or not? Analysing positional data from animal movement paths. *Dispersal, individual movement and spatial ecology: a mathematical perspective* (eds. M.A. Lewis, P.K. Maini & S.V. Petrovskii), vol. 2071 of *Lecture Notes in Mathematics*. Springer-Verlag, Berlin, Germany.

Plank, M.J. & Codling, E.A. (2009) Sampling rate and misidentification of Lévy and non-Lévy movement paths. *Ecology*, **90**, 3546–3553.

Plank, M.J. & James, A. (2008) Optimal foraging: Lévy pattern or process? *Journal of the Royal Society Interface*, **5**, 1077–1086.

Pyke, G.H. (2015) Understanding movements of organisms: it's time to abandon the Lévy foraging hypothesis. *Methods in Ecology and Evolution*, **6**, 1–16.

R Core Team (2015) *R: A Language and Environment for Statistical Computing.* R Foundation for Statistical Computing, Vienna, Austria.
URL `http://www.R-project.org/`

Regular, P.M., Hedd, A. & Montevecchi, W.A. (2013) Must marine predators always follow scaling laws? Memory guides the foraging decisions of a pursuit-diving seabird. *Animal Behaviour*, **86**, 545–552.

Reynolds, A. (2015) Liberating Lévy walk research from the shackles of optimal foraging. *Physics of Life Reviews*, **14**, 59–83.

Schick, R.S., Loarie, S.R., Colchero, F., Best, B.D., Boustany, A., Conde, D.A., Halpin, P.N., Joppa, L.N., McClellan, C.M. & Clark, J.S. (2008) Understanding movement data and movement processes: current and emerging directions. *Ecology Letters*, **11**, 1338–1350.

Senft, R.L., Coughenour, M.B., Bailey, D.W., Rittenhouse, L.R., Sala, O.E. & Swift, D.M. (1987) Large herbivore foraging and ecological hierarchies. *BioScience*, **37**, 789–799.

Sims, D.W., Humphries, N.E., Bradford, R.W. & Bruce, B.D. (2012) Lévy flight and Brownian search patterns of a free-ranging predator reflect different prey field characteristics. *Journal of Animal Ecology*, **81**, 432–442.

Smouse, P.E., Focardi, S., Moorcroft, P.R., Kie, J.G., Forester, J.D. & Morales, J.M. (2010) Stochastic modelling of animal movement. *Philosophical Transactions of the Royal Society B*, **365**, 2201–2211.

Sokal, R.R. & Rohlf, F.J. (1981) *Biometry*. W.H. Freeman, New York, USA, 2nd edn.

Stirling, I. (1999) *Polar bears*. Fitzhenry & Whiteside, Markham, Canada.

Stirling, I. & Derocher, A.E. (2012) Effects of climate warming on polar bears: a review of the evidence. *Global Change Biology*, **18**, 2694–2706.

Switzer, P.V. (1993) Site fidelity in predictable and unpredictable habitats. *Evolutionary Ecology*, **7**, 533–555.

Thiemann, G.W., Derocher, A.E., Cherry, S.G., Lunn, N.J., Peacock, E. & Sahanatien, V. (2013) Effects of chemical immobilization on the movement rates of free-ranging polar bears. *Journal of Mammalogy*, **94**, 386–397.

Tracz, B.V., LaMontagne, J.M., Bayne, E.M. & Boutin, S. (2010) Annual and monthly range fidelity of female boreal woodland caribou in response to petroleum development. *Rangifer*, **30**, 31–44.

Tyson, R.C., Wilson, J.B. & Lane, W.D. (2011) Beyond diffusion: Modelling local and long-distance dispersal for organisms exhibiting intensive and extensive search modes. *Theoretical Population Biology*, **79**, 70–81.

Viswanathan, G.M., Buldyrev, S.V., Havlin, S., Luz, M.G.E.D., Raposo, E.P. & Stanley, H.E. (1999) Optimizing the success of random searches. *Nature*, **401**, 911–914.

Weimerskirch, H., Guionnet, T., Martin, J., Shaffer, S.A. & Costa, D.P. (2000) Fast and fuel efficient? Optimal use of wind by flying albatrosses. *Proceedings of the Royal Society B*, **267**, 1869–1874.

Zollner, P.A. & Lima, S.L. (1999) Search strategies for landscape-level interpatch movements. *Ecology*, **80**, 1019–1030.

Zucchini, W. & MacDonald, I.L. (2009) *Hidden Markov models for time series: an introduction using R*, vol. 110 of *Monographs on Statistics and Applied Probability*. Chapman and Hall/CRC, Boca Raton, USA.

The following online Supporting Information is available for this article.

Appendix S1 Variation in threshold angle

Appendix S2 Model fit for each individual

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: $\psi_{\text{T}}(l)$, $v_0(\theta)$, $\phi(l)$, and $v(\theta)$, see Table 2.

Model	Likelihood function	k
TLW	$\prod_{t=1}^{n} \psi_{\text{T}}(l_t \mid \mu_{\text{T}}, a, b)\ v_0(\theta_t)$	3
BW	$\prod_{t=1}^{n} \phi(l_t \mid \lambda, a)\ v_0(\theta_t)$	3
CRW	$\prod_{t=1}^{n} \phi(l_t \mid \lambda, a)\ v(\theta_t \mid \kappa)$	4
CCRW$_{\text{A}}$	$\prod_{t=1}^{n} \Gamma_t \begin{pmatrix} \phi(l_t \mid \lambda_{\text{I}}, a)\, v_0(\theta_t) & 0 \\ 0 & \phi(l_t \mid \lambda_{\text{E}}, a)\, v(\theta_t \mid \kappa_{\text{E}}) \end{pmatrix} \begin{pmatrix} 1 \\ 1 \end{pmatrix}, \quad \Gamma_t = \begin{cases} \begin{pmatrix} \delta_{\text{I}} & 1-\delta_{\text{I}} \end{pmatrix} & \text{if } t = 1 \\ \begin{pmatrix} \gamma_{\text{II}} & 1-\gamma_{\text{II}} \\ 1-\gamma_{\text{EE}} & \gamma_{\text{EE}} \end{pmatrix} & \text{otherwise} \end{cases}$	7
CCRW$_{\text{L}}$	$\prod_{t=1}^{n} \Gamma_t \begin{pmatrix} \phi(l_t \mid \lambda_{\text{I}}, a)\, v_0(\theta_t) & 0 \\ 0 & \phi(l_t \mid \lambda_{\text{E}}, a)\, v(\theta_t \mid \kappa_{\text{E}}) \end{pmatrix} \begin{pmatrix} 1 \\ 1 \end{pmatrix}, \quad \Gamma_t = \begin{cases} \boldsymbol{\delta}\ ^{\dagger} & \text{if } t = 1 \\ \begin{pmatrix} 0 & 1-\gamma_{\text{I}}(1) & \dots & 0 & \gamma_{\text{I}}(1) & \dots & 0 \\ \vdots & \ddots & \ddots & \vdots & \vdots & \dots & \vdots \\ 0 & 0 & \dots & 1-\gamma_{\text{I}}(m-1) & \gamma_{\text{I}}(m-1) & \dots & 0 \\ 0 & 0 & \dots & 1-\gamma_{\text{I}}(m) & \gamma_{\text{I}}(m) & \dots & 0 \\ \gamma_{\text{E}}(1) & 0 & \dots & 0 & 1-\gamma_{\text{E}}(1) & \dots & 0 \\ \vdots & \vdots & \dots & \ddots & \ddots & \ddots & \vdots \\ \gamma_{\text{E}}(m-1) & 0 & \dots & 0 & 0 & \dots & 1-\gamma_{\text{E}}(m-1) \\ \gamma_{\text{E}}(m) & 0 & \dots & 0 & 0 & \dots & 1-\gamma_{\text{E}}(m) \end{pmatrix} ^{\ddagger} & \text{otherwise} \end{cases}$	6

[†] As in Langrock *et al.* (2012), we are using the stationary distribution for the initial values, $\boldsymbol{\delta}$, of the Markov chain for CCRW$_{\text{L}}$.

[‡] As in Langrock *et al.* (2012), $\gamma_{\text{I}}(r) = \frac{p_{\text{I}}(r)}{(1-\sum_{k=1}^{r-1} p_{\text{I}}(r))}$ and $\gamma_{\text{E}}(r) = \frac{p_{\text{E}}(r)}{(1-\sum_{k=1}^{r-1} p_{\text{E}}(r))}$. For both phases, we are using a Poisson distribution, $p_{\text{I}}(r)$ and $p_{\text{E}}(r)$, 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 θ represent step length and turning angle, respectively.

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

[†] Unlike in Auger-Méthé *et al.* (2015), we are not placing restrictions on the estimated μ_{T} values.

[‡] 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.

[§] 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$_\mathrm{A}$, and CCRW$_\mathrm{L}$	0.053	0.0030	0.023
γ_II	Probability of remaining in the CCRW$_\mathrm{A}$'s intensive phase	1.00 (0.98-1.00)	0.54 (0.44-0.64)	0.83 (0.78-0.88)
γ_EE	Probability of remaining in the CCRW$_\mathrm{A}$'s extensive phase	0.97 (0.89-1.00)	0.85 (0.80-0.90)	0.96 (0.96-0.97)
κ_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)
λ (km^{-1})	Rate parameter of the exponential distribution of the BW	0.43 (0.36-0.50)	–	–
λ_I (km^{-1})	Rate parameter of the CCRWs' intensive phase	7.7 (1.2-18.1)	53 (35-82)	16 (13-21)
λ_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)
α_I	Mean of the Poisson for CCRW$_\mathrm{L}$'s intensive phase	15 (10-19)	0.28 (0.13-0.53)	13 (9-16)
α_E	Mean of the Poisson for CCRW$_\mathrm{L}$'s extensive phase	14 (9-19)	4.0 (3.3-5.2)	17 (15-19)

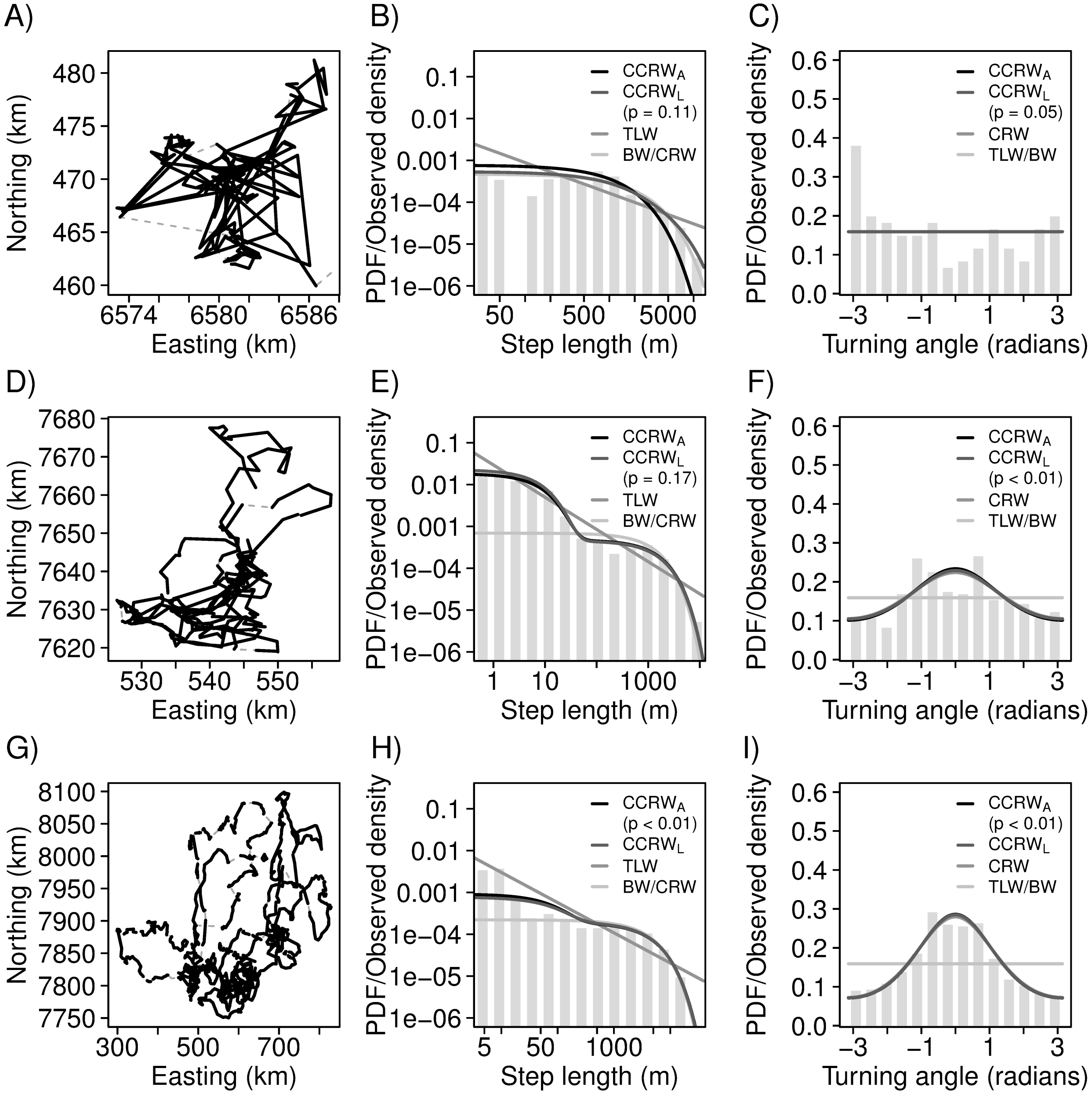

Figure 1: Fit of the models on the movement path of each species: (A-C) caribou, (D-F) grizzly, and (G-I) polar bear. (A, D, G) black lines represent the movement path using the 10° threshold angle and the gray dashed line the missing data. (B, E, H) Step length frequency with the probability density 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$_\text{A}$ or CCRW$_\text{L}$ with Akaike weight: $w_{\text{CCRW}} > 0.99$. 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.