WALKING IN THEIR FOOTSTEPS: NEW APPROACHES TO IDENTIFY BEHAVIOURAL PROCESSES AND DEFINE HOME RANGES USING ANIMAL MOVEMENT DATA

by

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A thesis submitted in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

in

Ecology

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Abstract

Animal movement and space-use patterns influence the distribution and abundance of species, predator-prey interactions, and many other ecological processes. Different approaches are used to study individual's space-use strategies and each approach suffers from unique challenges. The mechanistic underpinning of some movement models have led many to confuse patterns with process, while coarse space-use analyses have led many to miss critical aspects of animal behaviour. In this thesis, I address these challenges by refining models of animal search strategies and developing new methods to incorporate drift in home range analyses.

Understanding how animals find resources with incomplete information is a topic of interest and controversy in ecology. Two search strategies have become prominent: the Lévy walk and area-restricted search (ARS). Although the processes underlying these strategies differ, they can produce similar movement patterns and current methods cannot reliably differentiate between them. I present a method that can simultaneously assess the strength of evidence for these two strategies, and assess the empirical support for the use of each strategy by a range of species: woodland caribou (*Rangifer tarandus caribou*), grizzly bears (*Ursus arctos*), and polar bears (*U. maritimus*). Although previous methods would have found evidence for the Lévy strategy, my method shows greater support for the ARS strategy. My results also show that species and individuals vary in their search strategies. While the ARS was sufficient to explain the movement of some caribou and grizzly bears, none of the models examined adequately explained the movement of polar bears. These results demonstrate the usefulness of this method when evaluating the evidence for the Lévy and ARS strategies, and highlight the need for additional mechanistic search strategy models.

A home range represents the area an animal use to perform the majority of the activities required for survival and reproduction. As such, measuring home range size has been an important tool to quantity the amount of habitat an animal requires. However, in moving habitats, traditional home range estimates may be ill-suited to this task. I present a new approach to estimate the amount ice habitat encountered by polar bears. These estimates showed that the traditional geographic home range underestimates both the movement of bears and the amount of ice habitat that they encounter. The results also indicated that bears living on highly mobile ice might be exposed to higher energetic costs, and potentially larger energetic gains, than bears inhabiting more stable ice.

By improving methods to identify search strategies and developing new approaches to investigate the effects of drift on animal home ranges, I provide ecologists a set of new tools to study animal space use and contribute to the flourishing field of movement ecology.

Preface

This thesis is an original work by Marie Auger-Méthé. Some of the research included in this thesis was conducted as part of collaborations. Chapter 2 was written with the guidance of Dr. Colleen Cassady St. Clair at the University of Alberta. The analytical techniques of chapter 3-4 were developed with the assistance of Dr. Edward A. Codling at the University of Essex and Dr. Michael J. Plank at the University of Canterbury, both of whom also provided feedback on these chapters. The caribou data of chapter 4 was collected by Craig DeMars, who also contributed feedback on the chapter. The literature review in chapters 1 and 6, and the analysis in chapter 5 are my original work.

Chapter 2 of this thesis has been published as: Auger-Méthé, M., C.C. St. Clair, M.A. Lewis, and A.E. Derocher. 2011. Sampling rate and misidentification of Lévy and non-Lévy movement paths: comment. Ecology 92:1699-1701. This is a critic of a published article. I lead the development of the arguments and the manuscript composition. Dr. St. Clair was involved in concept formation and manuscript composition. Drs. Mark A. Lewis and Andrew E. Derocher are supervisory authors and provided feedback on the manuscript.

The data collected specifically for this research project was approved by the University of Alberta BioSciences Animal Policy and Welfare Committee - Protocols #600904, #6001004, #6000312.

To Devin

Acknowledgements

I am extremely grateful to my two PhD advisors, Drs. Mark Lewis and Andrew Derocher, both of whom are exceptionally supportive, generous and talented teachers. When I joined Mark's lab, I had close to no modeling skills; only a blurred memory of high school math and some knowledge of basic statistical tests. Thanks to Mark's contagious enthusiasm for mathematical biology, I have not only learned tremendously, I now have a completely new appreciation for quantitative ecology. Mark's enthusiasm is manifested in many aspects of his scientific work, but is particularly striking in his teaching style and his efforts to foster a research group that is dynamic, rigorous, respectful, and incredibly enriching. I came to the University of Alberta to learn mathematical modeling skills and Mark helped me learned more than I thought possible. I am incredibly grateful for Andy's genuine care for students. I always knew Andy had my best interests in mind, that he fully believed in me, and that he would go out of his way to help me succeed. I have seen him take many decisions that were clear indications that he wants a PhD to be centered on the student's aspirations rather than his owns. Academia is difficult and competitive, and it is rare to find people like Andy that have an open door, remove as many obstacles as possible for their students, and make sure they get the most out of their degrees.

I also had the privilege to be guided by many other professors. I am particularly thankful to my committee members Drs. Evelyn Merrill and Subhash Lele, who were both rigorous and supportive throughout my thesis. I was also greatly inspired by Dr. Colleen St. Clair, a great female role-model who encouraged me to be fierce in science and to write my first critical scientific piece. I am also thankful to Drs. Edward Codling and Michael Plank for the help provided on many chapters and the extremely generous offer to collaborate on multiple other projects. In addition to being thankful for their intellectual input, I am grateful for their openness and willingness to collaborate with me, despite my criticism of their work.

I am also thankful to my fellow students and postdocs. I am particularly thankful to Ulrike Schlägel who had the patience and the German precision to walk me through the many equations that stumped me. I am also indebted to Craig DeMars who shared some of his data, help me understand caribou behaviour, and invited me to collaborate in one of my favourite side projects. I am also very thankful for Dr. Jonathan Potts, who invited me to work on my other favourite side project and was always very supportive. I am also thankful to all members of the Eco Modeling group, with a special thanks to Devin Goodsman and Stephanie Peacock. I have learned so much from this journal club that it created expectations that are unlikely to be met by others. I was fortunate to be part of two great labs. I am thankful for all field support and great lab beers with the Derocher lab and for all the modelling support and great lab lunches with the Lewis lab.

I am thankful to Alberta Innovates - Technology Futures, Andrew Stewart Memorial funds, Steve & Elaine Antoniuk Memorial funds, Natural Sciences and Engineering Research Council of Canada, and the University of Alberta for their scholarships and awards. The research was funded by the Aquarium du Québec, ArcticNet, Bureau of Ocean Energy Management, Canada Research Chairs program, Canadian Association of Zoos and Aquariums, Canadian Circumpolar Institute, Canadian Wildlife Federation, ConocoPhillips (North) Canada Limited, Environment Canada, Hauser Bears, Inuvialuit Land Claim Wildlife Studies Implementation Fund, Killam trusts, Natural Sciences and Engineering Research Council of Canada, Northern Scientific Training Program, Northwest Territories Department of Environment and Natural Resources, Pittsburgh Zoo, Polar Continental Shelf Project, Polar Bears International, Quark Expeditions, and World Wildlife Fund (Canada). Some of the field work was conducted by Dennis Andriashek, Craig DeMars, Mark Edwards, Nicholas Lunn, and Evan Richardson, to whom I am thankful.

I am extremely thankful for the support of my family, in particular for the love and encouragement of my mom, dad, and godfather. My family had a trying five years, with many losses and difficulties, but despite these hardships and many thousands of km of distance I always had their unconditional support.

Finally, I want to thank the most important person in my life, Devin. Devin read every line of this thesis (probably multiple times) and gave invaluable comments throughout my PhD. I could not have done this PhD without Devin's continuous care, help, and love. He made sure I ate (absolutely wonderful food), he read boring books to me so I could fall asleep at night, and he was always incredibly supportive.

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Chapter 1

Feedbacks between scales of animal space use: studying both movement strategies and ranging patterns is essential to understand their dynamics

The movement and space-use patterns of animals have important consequences for many ecological processes. They not only affect the distribution of species, they have the potential to influence population abundance, predator-prey dynamics, disease transmission, as well as community and ecosystem structure (Börger et al., 2008; Nathan et al., 2008). For example, dispersal strategy can influence important aspects of population dynamics, such as the extinction-colonisation balance of metapopulations (Bowler and Benton, 2005). Seasonal migrations of herbivores outside their predators' range can affect the population dynamics of other species, including their predators and the alternative resident prey that predators are forced to rely on (Fryxell and Sinclair, 1988). Both long-distance movement and home range behaviours can affect disease transmission (Altizer et al., 2011; Habib et al., 2011; Schauber et al., 2007). For instance, home range overlap can increase direct and indirect contact rates between individuals and thus increase disease transmission (Habib et al., 2011; Schauber et al., 2007). Because drivers of home range size and overlap are tightly linked to individuals' energetic needs, habitat quality, and population density (Jetz et al., 2004), home range behaviours and patterns can be used to predict a variety of broader scale ecological patterns. Some ecologists define a species' geographic range as the area encompassing the home ranges of all individuals in the population (Gaston, 1991).

Others predict community structure in heterogeneous landscapes using the spatial distribution of home ranges constructed according to body size, resources needs and costs of locomotion (Buchmann et al., 2011). Because movement and home range patterns affect a plethora of ecological processes, it is important to understand the mechanisms driving varied space-use strategies and the links between them.

The basic drivers of individuals' space-use strategies will be the trade-offs between acquiring the resources required for survival and reproduction, and limiting the costs and risks associated with acquiring these resources (e.g., Adams, 2001; Mitchell and Powell, 2004; Zollner and Lima, 1999). Individuals require a variety of resources, including food, mates, and shelters (Bell, 1991). The importance of these resources in shaping the space-use behaviour of individuals will vary with species, sex, age class and reproductive status (Bell, 1991; Law and Dickman, 1998; Maher and Lott, 2000). Moreover, the costs and risks associated with resource acquisition will depend on factors such as the spatial distribution of resources, number of competitors, and presence of predators (Bell, 1991; Grant, 1993; Maher and Lott, 2000).

There is a hierarchy of trade-offs to consider (Fig. 1.1). At the higher level, animals need to trade-off the energy and time devoted to acquiring different resources, as well as other important activities such as escape from predation and offspring care (e.g., Houston et al., 2012; Markman et al., 2002). These trade-offs affect not only the time, energy, and behavioural budgets of these animals, they also influence their spatial patterns (Bernstein and Jervis, 2008; Heithaus and Dill, 2002; Mysterud and Ims, 1998). At the lower level, individuals need to balance the costs and benefits associated with a specific activity. For example, territorial defence helps an individual maintain exclusive access to resources, but evicting intruders increases energy expenditure and the risk of injuries (Low, 2006; Riechert, 1988). Such trade-offs are reflected in the movement behaviours of species that chases intruders over different distances depending on the intruder's characteristics (e.g., Kohda, 1991; Whiting, 1999). These lower level trade-offs can also be exhibited in the choice of movement strategies used for a specific activity, such a searching for food (Fig. 1.1B). In general, many movement and home range models focus on the energetic benefits of acquiring food resources and the locomotion costs associated with reaching them (e.g., Mitchell and Powell, 2004; Rhodes et al., 2005; Van Moorter et al., 2009; Zollner and Lima, 1999). Each of the two levels in the hierarchy of trade-offs is more closely associated with a particular scale of space use (Fig. 1.1). At the lower level, small-scale movement models can specify detailed movement rules and trade-offs involved in performing one activity, or perhaps a small set of activities. Home range analysis and other larger-scale space-use patterns are a composite of all behavioural activities and higher level trade-offs.

1.1 Bottom-up approach: using movement models to understand animal space use

Ecologists can examine movement and space-use patterns in a bottom-up approach: understanding the mechanisms of movement strategies before linking them to emergent space-use patterns. A recent unifying paradigm for movement ecology proposed that movement is composed of four mechanistic components: the internal state, the motion capacity, the navigation capacity, and external factors (Nathan et al., 2008). We can relate each of these building blocks to the motivations, constraints, costs, and benefits underlying varied movement strategies. The internal state quantifies the motivation for a specific set of activities (e.g., searching for food, mating) and could, for example, be used to represent the behavioural trade-offs or resulting energy/time budget of an individual. The motion capacity reflects the different physiological constraints on an individual's movement. For example, how far can a fish swim and how far can it drift with the current. The navigation capacity represents the ability to use perception or memory to create goal-oriented movement. The external factors encompass abiotic (e.g., temperature and currents) and biotic factors (e.g., presence of competitors or predators) that can affect movement. External factors have the potential to affect all other components of movement. For example, a snowstorm might reduce an animal's motivation to forage, its ability to walk long distances, and its capacity to perceive visual or auditory cues. All of the components of this framework are interrelated to describe the movement strategies for a set of behaviours, and the resulting lifetime movement path emerges from this set of movement rules.

Other ecologists have divided movement into similar components, but with a focus on the ranging patterns they form. Mueller and Fagan (2008) divided movement into non-oriented, oriented, and memory-based mechanisms. They argued that spatiotemporal dynamics in resource distributions affect the benefits gained from these movement mechanisms, which in turn shape population-level ranging patterns. Börger et al. (2008) discussed the four important components that lead to the emergence of stable home ranges: focal point attraction, memory effects, habitat and resource distributions, and social interactions. For example, models that incorporate wolves' (*Canis lupus*) attraction to den sites, territory marking behaviours, and prey distribution can predict the stable boundaries between the territories of different packs (Lewis and Murray, 1993; White et al., 1996). The assumption of these modeling frameworks is that ranging patterns emerge out of the specific movement behaviours. Although this is consistent with Burt's (1943) definition of a home range as an area used by an animal for its usual activities such as foraging, mating and caring for offspring, it does not reflect how specific ranging patterns might, in turn, affect the benefits gained from specific movement strategies.

1.2 Top-down approach: using broad scale patterns to inform movement models

While it is clear that the movement strategies of an individual will influence its space use, we can also take a top-down approach and investigate how different space-use behaviours can affect the costs and benefits of movement. A simple, intuitive example is how the territorial behaviour of an animal will affect most aspects of its movement. A territorial animal will largely restrict its search for food and mates to its territory, will spend time patrolling its periphery, and will chase away intruders. Other space-use behaviours also have the potential to affect animal movement, albeit in potentially subtler manners. While memory is likely an important process in the formation of a stable home range (Börger et al., 2008; Van Moorter et al., 2009), one could also argue that memory-based search strategies might emerge because animals have stable home ranges. The emergence of a stable home range could be the results of a spatial anchor, such as a nest site. In fact, as Börger et al. (2008) explained, most models that lead to emergence of stable home ranges only do so because of the presence of a fixed point of attraction. Due to this spatial anchor, a central-place forager is repeatedly exposed to the same environment, allowing the animal to memorise spatial information and develop a memory-based foraging strategy. Some ecologists have argued that territories and home ranges exist as cognitive maps in animals' brains and that animals use them to make movement decisions (Fagan et al., 2013; Powell and Mitchell, 2012).

The top-down approach is used extensively in studies investigating the importance of different habitat types to animals (e.g., Aebischer et al., 1993; Johnson, 1980; Meyer and Thuiller, 2006). Johnson (1980) proposed that habitat selection at a given scale is conditional on selection at larger spatial scales. Within this framework, an animal first selects a home range based on general habitat preference. Then, the animal selects for specific habitat types based on the availability of these within their home range. Thus, the movement decisions made at relatively small spatiotemporal scales are highly dependent on the larger space-use decision made by an individual. For example, how far an animal is from the home range centre was shown to alter the probability of moving into different habitat types (Rhodes et al., 2005). Animals are not necessarily free to choose an optimal location for their home range. Whether and where an animal will disperse is dependent on many factors and constraints (Bowler and Benton, 2005). For example, the quality and size of territories of Eurasian beaver (*Castor fiber*) decline with settlement date because good territories are claimed first (Campbell et al., 2005). Because displacing a home range can incur high costs and mortality risk, animals have a tendency to remain in potentially suboptimal home ranges, unless there are drastic changes in the environment (e.g., Isbell et al., 1990; McDougall and Kramer, 2007; Morris, 1987). Thus, without capturing the dispersal and establishment phases, it is difficult to infer an individual's large-scale home range selection based on its smaller scale movement decisions.

In addition to affecting which resources are available to an individual, the establishment of a home range has the potential to alter the distribution of the resources themselves. For example, wolf predation can cause prey densities to be highest in the buffer zone between the territories of neighbouring packs (Lewis and Murray, 1993; White et al., 1996). Such patterns result from the heavier use within the home range, and the avoidance of aggressive encounters with neighbours. Resource depletion within the home range has also been observed in non-territorial animals. For example, "Ashmole's halo" is a zone of local food depletion surrounding seabird colonies (Elliott et al., 2009; Gaston et al., 2007). By affecting resource distributions within their home range, individuals are required to alter their movement strategies. For example, as the size of the Ashmole's halo increases through time, seabirds are forced to travel longer distance to forage (Elliott et al., 2009; Lewis et al., 2001).

1.3 Importance of using both approaches

As I hope I have conveyed above, there are feedbacks between larger scale space-use patterns and smaller scale movement strategies. Ideally ecologists could address both scales in a single cohesive framework and this may be the eventual outcome of the new and ambitious movement ecology paradigm (Nathan et al., 2008). However, for this bottom-up approach to be sufficient by itself, it would require modeling an individual's complete set of movement behaviours, including rare events such as dispersal, and how the individual alters the environment. For such an endeavour to be feasible, it will require new techniques that handle complicated feedbacks, such as the dynamic relationships between the resources distribution and animal movement, and multiple levels of hidden states, such as the memory maps of individuals. Independently addressing some of these aspects, such as modeling the hidden memory process, is already challenging (Fagan et al., 2013). Tackling all of them simultaneously, and applying such models to data, represents a formidable challenge. Thus, in the meantime, one way to incorporate the effects of spatial patterns on movement and to increase our understanding of both scales is to continue to refine both approaches.

While studying small-scale movements and large-scale space-use patterns are both useful, each involves unique challenges. With smaller scale studies it is possible to model the details of a behavioural strategy and infer whether there is evidence for it by applying the model to data. However, such approaches can be misused. The mechanistic underpinning of such models has misguided many to confound pattern with process. In particular, different movement strategies, such as the Lévy walk and the Area Restricted Search (ARS), can produce similar movement patterns even though their underlying behavioural mechanisms differ (Benhamou, 2007). Differentiating between these two strategies is challenging, and identifying whether they are a good reflection of animal behaviour has proven difficult. Large-scale analyses facilitate the understanding of broader scale ecological processes because they summarise the results of all the behaviours expressed by animals over the period of the analysis. However, such summarisation can obscure important features, such as the spatiotemporal variation in resource distributions and the effects of currents on observed patterns. While wind and water currents affect movement strategies (e.g., Campbell et al., 2010; Klaassen et al., 2011), their influence is rarely incorporated in analyses of broader space-use patterns. In my thesis, I address problems in the analysis of animal movement and space-use pattern at both scales.

1.4 Dissertation outline

Chapters 2-4 address multiple aspects related to the difficulties in differentiating between the movement patterns created by two of the most prominent search strategies in the literature: the Lévy walk and the ARS. As mentioned above, these two popular random search strategies differ in their underlying behaviours, but create similar movement patterns. In Chapter 2, I start by identifying the problems associated with differentiating between these two strategies and suggesting potential solutions. This is in the form of a comment on Plank and Codling (2009), a paper demonstrating that current methods would misidentify the movement generated by an ARS as being evidence for the Lévy walk. I argue that comparing the relative fit of the Lévy walk against a null model is insufficient for the identification or misidentification of a movement process. To differentiate the Lévy walk from the ARS, we need to develop a simple likelihood function for the ARS. In addition, it is important to recognize that the best model according to relative measures of fit might still be a poor representation of the underlying process. Thus, a minimum requirement for assessing whether a movement pattern is consistent with a process is a verification of the absolute fit of this model.

In Chapter 3, I develop comparable likelihood functions to represent the Lévy walk and the ARS. Unlike previous attempts to do so, these likelihood functions include both important measures of movement: the turning angles and the steps lengths. My model for the ARS is a hidden Markov model that incorporates autocorrelation in behaviour, which is a hallmark of the intensive phase of the ARS. These likelihood functions can be used to assess both the relative fit of the models (i.e., identify the best model) and the absolute fit (i.e., verify whether the best model adequately explains the data). Through a simulation study, I show that my method allows one to differentiate between the ARS and the Lévy walk. I show that it can be easily applied to real animal movement data, by using a small and complex data set from polar bears (*Ursus maritimus*) from Hudson Bay, Canada.

In Chapter 4, I use the method developed in Chapter 3 to assess the evidence for the Lévy walk and ARS strategies in the movement data of three species: the polar bear, grizzly bear (*U. arctos*), and woodland caribou (*Rangifer tarandus caribou*). I show that, although previous methods would have found some evidence for the Lévy walk, there is stronger support for the ARS than for the Lévy walk in these three species. The strength of the support for the ARS varies among species and individuals. The ARS is sufficient to describe the movement of some, but not all, individuals. Random search models might be inappropriate for these animals, indicating a need to develop search strategy models that incorporate factors such as their perceptual and cognitive capacities. For species that inhabit a habitat with currents, such as polar bears on the drifting sea ice, movement models will also need to differentiate between voluntary movement and drift.

In Chapter 5, I move away from random search strategies and investigate the effects of drift on polar bear home ranges. Home range size estimates are often used to assess the amount of space required for animals to perform the activities essential for their survival and reproduction. While traditional home range size estimates based on geographic locations are an adequate representation of the space required by terrestrial species, they are inadequate for animals living in drifting habitats. In particular, traditional home range estimates are inaccurate representations of the amount of sea ice encountered by a polar bear. The sea ice is the prime foraging habitat of the bear, and estimating the amount of ice encountered by bears may provide a better approximation of the habitat space they require. In this Chapter, I develop a technique to make these estimates. I demonstrate that polar bears encounter larger areas of ice habitat that traditional home range estimates would suggest, and that the amount of ice habitat encountered increases with drift. Moreover, when investigating correlates of home range size, I show that it is possible to explain more of the variation in the area of ice habitat used by individuals than in their geographic home range size.

In Chapter 6, I conclude by discussing how this work can inform research on species-habitat relationships. Many movement models used to identify foraging behaviours are based on search strategy theory, but their predicted foraging areas are not always linked to known foraging events. Correctly specifying animal search strategies is essential if ecologists are to accurately identify foraging habitats using movement data. Many animals exploit the moving habitats of oceans, rivers, and the atmosphere. Incorporating drift into home range models for these species will provide a more accurate understanding of their habitat use. My work contributes new approaches and ideas to the flourishing field of movement ecology. While movement ecology is providing unprecedented insights into how animals interact with their environment, I believe that coupling these new developments to fitness data is the key to moving beyond pattern description, and towards an understanding of their broader ecological and evolutionary significance.

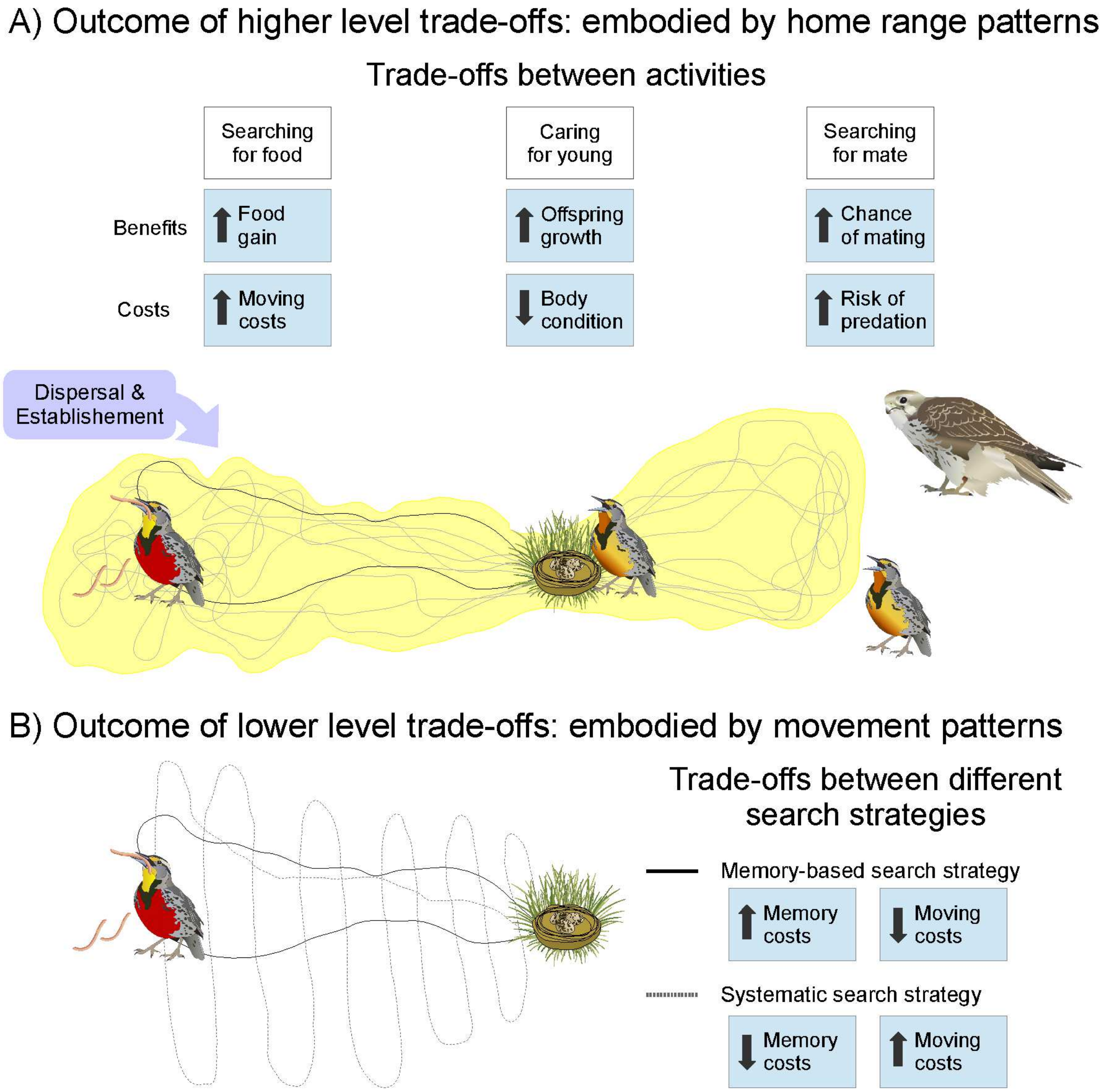

Figure 1.1: A depiction of the relationship between the hierarchy of behavioural trade-offs and their associated scales of space use. Panel A represents the outcome of the higher level trade-offs and portrays a fictitious male bird (red bird) that must balance foraging, taking care of his offspring and mate (nest with yellow bird), and finding extra-pair copulation opportunities (other yellow bird), without getting eating by a predator (raptor). The results of the higher level trade-offs are best summarised spatially by the home range pattern (yellow polygon). Panel B represents how a single movement bout (black line or grey line) embodies the outcome of the lower level trade-offs between the costs and benefits of a given activity, such as forging trip. Created with symbols courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/)

Chapter 2

Sampling rate and misidentification of Lévy and non-Lévy movement paths: Comment[†]

In a recent paper, Plank and Codling (2009) critique the use of Lévy walks to describe animal movement, arguing that non-Lévy walk processes could be misidentified as Lévy patterns and, conversely, movement patterns actually generated by Lévy processes may be wrongly attributed to other mechanisms. The authors suggest that this ambiguity is partly caused by sampling paths at scales that do not reflect actual movement decisions and this despite the theoretical scale-independence of Lévy walks. These findings, if true, would be an important contribution, as the Lévy walk is a popular, although controversial, model in the animal movement literature.

Here, I support Plank and Codling's (2009) contention that movement patterns must be attributed to the correct process and that animal movement is likely not truly scale-invariant. However, I challenge their methodology, and hence that they showed that Lévy and non-Lévy processes could be misidentified for one another and that this ambiguity partly depends on the sampling scale. My main criticism is that using the relative fit of poorly chosen models, without verifying for the absolute fit of the best model, is insufficient evidence for either the identification or the misidentification of a process. To demonstrate this methodological problem, I first describe the models used to simulate the data and thus representing the movement processes. Then I describe how the models that were fitted to the data differed from the ones used to

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[†] A version of this chapter has been published as: Auger-Méthé, M., C. C. St. Clair, M. A. Lewis, and A. E. Derocher. 2011. Sampling rate and misidentification of Lévy and non-Lévy movement paths: Comment. Ecology 92:1699-1701.

simulate the data. Finally, I argue that the authors failed to consider the importance of examining the absolute fit of the best model. Without this information, it is impossible to determine whether either model provides a reasonable explanation for a given data set, whether those data are generated by simulations or actual animals.

2.1 Simulating ecological processes: the movement simulations of Plank and Codling (2009)

Plank and Codling (2009) simulated two types of datasets: one representing a Lévy walk and one representing a composite correlated random walk (CCRW). To simulate the Lévy walk they used a non-correlated random walk with a truncated Pareto distribution for the step length distribution. The CCRW was chosen as an alternative movement process to the Lévy walk because this distinct behavioral process produces a similar movement pattern to the Lévy walk (Benhamou, 2007; Plank and James, 2008). The CCRW was composed of two phases: an intensive phase with tortuous movement and small step lengths and an extensive phase with nearly straight movement with long step lengths.

2.2 Discrepancy between the models used to simulate the processes and those to explain the patterns

The two models Plank and Codling (2009) fitted to recover the simulated process differed from those used to produce the data, making it likely that the absolute fits of these models would be poor. The authors fitted a non-truncated Pareto distribution to recover a process simulated with the truncated version of this distribution. The non-truncated distribution is scale-invariant at all measurable scales. In contrast, the truncated Pareto distribution has an upper limit on the size of the step lengths and is thus only scale-invariant for a limited range of scales. Plank and Codling (2009) state that they used the non-truncated Pareto distribution to fit the data because it is the distribution most commonly used. However, most studies using the non-truncated Pareto distribution also used the now-obsolete histogram-based method to test for Lévy walks (but see Focardi et al., 2009). This histogram-based method did not allow for a truncated version of the Lévy walk. Because the more modern maximum likelihood method used by Plank and Codling (2009) allows to fit a truncated Pareto distribution (Edwards, 2008; White et al., 2008), the authors should have additionally fitted the truncated Pareto distribution to their simulated data.

Not only did Plank and Codling (2009) use two different models to simulate and recover the Lévy process, they used two different models to simulate and recover the CCRW. In this case these two models are not merely two different versions of the same model but completely distinct. Thus, the absolute fit is expected to be poor. They fitted an exponential distribution to recover a process simulated with CCRW. An exponential distribution is often used to model a simple random Poisson process and has been an alternative model against which Pareto distribution has been compared in Lévy walk studies (Edwards, 2008; Edwards et al., 2007; Humphries et al., 2010). However, the exponential distribution is not a good representation of a CCRW and we cannot expect the exponential distribution to adequately fit a CCRW. Plank and Codling (2009) state that they used the exponential distribution because the only likelihood function that could recover a CCRW process is complicated and uses Bayesian statistics (see Morales et al., 2004). This indicates the need for a simple likelihood function that describes the step length distribution of a CCRW.

2.3 Comparing two poor models with Akaike weights is insufficient evidence for process identification

The main goals of the study by Plank and Codling (2009) were to verify whether a Lévy walk can be misidentified for a Poisson process and whether CCRW can be misidentified as a Lévy walk. To do so, they compared the fit of the non-truncated Pareto and the exponential distributions using Akaike weights. By definition, Akaike weights can only measure the relative fit of the candidate models, not their absolute fit to the data (Burnham and Anderson, 2002). Thus, the best model according to Akaike weights may still be a poor model for the data. However, when the Akaike weights favored the wrong model, Plank and Codling (2009) concluded that a misidentification was likely to occur. For example, when Akaike weights favored the Pareto over the exponential distribution for data simulated with the CCRW, Plank and Codling (2009) concluded that the CCRW was likely to be misidentified as a Lévy walk.

For Plank and Codling (2009) to suggest that CCRW could be misidentified as a Lévy walk, they would have needed to investigate the absolute fit of the best model. While Akaike weights can identify the best of the candidate models, only a measure of absolute fit can identify whether the best model adequately fits data. In the articles that introduced Akaike weights as a method to compare Lévy walks to other movement models (Edwards, 2008; Edwards et al., 2007), goodness-of-fit tests (G-tests) were used to verify that the best model fitted the data. In other recent studies that applied Lévy walks to animal movement using maximum-likelihood methods similar to Plank and Codling (2009), the absolute fit was demonstrated by the analysis of the residuals (e.g., Focardi et al., 2009), statistical tests (e.g., Schreier and Grove, 2010), and by visual inspection of the fit of the best model to the data (e.g., Focardi et al., 2009; Humphries et al., 2010). Without such verification of absolute model fit, the conclusion that CCRW can be misidentified as Lévy walks is unwarranted.

A visual assessment of Fig. 3 in Plank and Codling (2009) suggests that neither the Pareto nor the exponential distribution fits the CCRW. This reveals that, even if the Pareto distribution fits the data simulated with a CCRW better than the exponential distribution according to Akaike weights, the Pareto distribution does not appear to adequately describe the CCRW. Whether a goodness-of-fit test, such as a G-test, would have confirmed such discrepancy needs to be investigated. Therefore, even though Plank and Codling (2009) importantly showed that Akaike weights can be misleading, their suggestion that CCRW is easily misidentified as a Lévy walk is unfounded. This reasoning also extends to their other conclusions, such as that a Lévy walk could be misidentified for a Poisson process and that the assumption of scale-invariance of Lévy walks is tenuous.

2.4 Conclusion

The important study by Plank and Codling (2009) appropriately cautions ecologists not to blindly assume that pattern is equivalent to process in the study of animal movement and that animal movement is likely not truly scale-invariant. Despite the identification of these potential problems, Plank and Codling (2009) have not provided definitive tests for their detection, and my analysis of their study should extend the caution to promote the investigation of both the relative and the absolute fit of movement models. Because Plank and Codling (2009) did not emphasize the importance of the absolute fit of the best model, they did not demonstrate whether a CCRW actually would be misidentified as a Lévy walk, or a Lévy walk as a Poison process. Nonetheless, Plank and Codling (2009) highlighted an important and perennial problem associated with applying the Lévy walk to empirical data. The Lévy walk is too often compared to simplistic alternative models, and rarely against strong alternative models. The two-phase search strategy associated with a CCRW produces a similar movement pattern as the Lévy walk strategy, yet the CCRW is rarely used as an alternative model in studies of Lévy walks. One reason for this tendency is that there is no simple likelihood function for CCRWs. A logical next step is to develop such a function so ecologists can rigorously compare the Lévy walk against this strong alternative model. By distinguishing between these two processes, we will be a step further in elucidating the mechanisms that diverse organisms, including humans, use to find resources.

Chapter 3

Differentiating between the Lévy and the area-restricted search strategies

3.1 Introduction

Search strategies that allow targets to be found with incomplete information are relevant to diverse fields of study (Bénichou et al., 2011). In particular, they have received much attention in the animal movement literature, where the two most prominent are the Lévy strategy and area-restricted search (ARS) strategy (Dragon et al., 2012; Fauchald and Tveraa, 2003; Viswanathan et al., 2008). The Lévy strategy is often represented by the Lévy walk, a popular but controversial movement model (e.g., Benhamou, 2007; Edwards et al., 2007; Humphries et al., 2012; Sims et al., 2012). The Lévy walk is defined as a random walk with a power-law distribution describing the step length frequency. This distribution has a characteristic heavy tail that allows for extremely long step lengths. The ARS (also known as area-concentrated search) strategy involves two behavioral modes and is used for animals searching in heterogeneous environments (Benhamou, 1992). It can be modeled with composite random walks (Benhamou, 2007). Such two-behavior models are often used to identify foraging events and to locate food patches from movement data (e.g., Dragon et al., 2012; Jonsen et al., 2007; Knell and Codling, 2012). Each behavior is related to a specific part of the landscape. The intensive search behavior is triggered by the encounter of a food item. This behavior is called ARS because the animal uses low speed and large turning angles to remain within a food patch and thus increase the probability of detecting prey. As this behaviour is key for the increase in prey detection, it gives its name to the overall strategy. The extensive search behavior is resumed after repeated unsuccessful searches. It uses fast and nearly straight movement to find the next food patch. Both the Lévy and the ARS strategies have been claimed to be optimal under certain conditions (Benhamou, 1992; Viswanathan et al., 1999, but see James et al. 2011) and both have empirical support (e.g., Dragon et al., 2012; Humphries et al., 2012).

Although the processes underlying these two search strategies differ widely in their biological interpretation, their movement patterns are similar and difficult to differentiate. Many have argued that the ARS strategy could be confounded with the Lévy strategy (Benhamou, 2007; Codling and Plank, 2011; Plank and Codling, 2009; Plank and James, 2008), and this, partly due to a lack of comparable models for these strategies (Chapter 2). In response, new methods to identify the Lévy strategy have been developed (Gautestad, 2012, 2013; Reynolds, 2012, but see Auger-Méthé et al. 2014). However, these improved methods cannot be used to quantify the evidence for the ARS strategy. Quantifying the level of evidence for each strategy is important as it both reduces the potential for misidentification and allows for a more comprehensive analysis of search strategies. Recently, methods have been proposed that simultaneously fit the Lévy walk and models approximating the ARS strategy (Jansen et al., 2012; Plank et al., 2013). Although these methods represent significant improvements over previous approaches, they do not fully represent the ARS strategy as they lack turning angles and temporal correlation in behaviors. Turning angles are an essential part of movement and are crucial for distinguishing between the two movement behaviors found in the ARS strategy (Benhamou, 1992). Temporal correlation in behaviors is an inherent characteristic of the ARS strategy because it is required to create the tortuous movement that allows the animal to remain in a food patch.

Here, I present a new method for differentiating between the Lévy and the ARS strategies. In the proposed method, the likelihood function for the ARS strategy is a hidden Markov model that incorporates turning angles and behavioral persistence (similar to Langrock et al., 2012). For comparability, the common likelihoods for the Lévy strategy and two null models are modified to incorporate turning angles. These likelihoods are created because they are essential for a set of statistical measures that assess both the relative and absolute support for each strategy. Using a simulation study, I show that my method can be used to successfully differentiate between the Lévy and ARS strategies and to assess the relative and absolute fit of the models. I demonstrate the applicability of my method by applying it to the movement paths of two polar bears (*Ursus maritimus*).

3.2 Methods

3.2.1 Development of the proposed method

My proposed method consists of likelihood functions representing each search strategy and statistical measures that use these likelihoods to assess the support for each strategy.

Likelihood functions

The likelihood functions use the information from both movement measures of a step at time t, $d_t = (l_t, \theta_t)$: step length, l_t, and turning angle, θ_t. The step length, l_t, is defined as the distance between the starting and ending locations of the step. The turning angle, θ_t, is defined as the angle of a step relative to the previous step direction. I focus on the case where the animal is moving (i.e., not resting), and so do not include steps with identical start and end points. Excluding these steps is possible because the models either assume that each measure of movement is independent and identically distributed or, in the case of the hidden Markov model, are built to handle missing steps. In this section, I present the development of the likelihood functions representing the ARS strategy, the Lévy strategy, and two null models. The four likelihoods differ mainly in the probability density functions (PDFs) chosen to describe the step length and turning angle frequencies.

Similar to others (e.g., Dragon et al., 2012; Plank and Codling, 2009), I represent the ARS by a composite correlated random walk (CCRW). A CCRW is a combination of two random walks, representing two behavioral modes. I describe the tortuous movement of the intensive search (hereafter denoted with subscript I) with a Brownian walk and the directed movement of the extensive search (hereafter denoted with subscript E) with a correlated random walk. The Brownian walk and correlated random walk are two common models that differ in their turning angle distribution. While an animal following a Brownian walk has no preferred turning direction, one following a correlated random walk has a tendency to continue in the same direction as the previous step (Codling et al., 2008). The differences between the two behaviors are incorporated in the likelihood function by ascribing them different turning angle and step length PDFs.

For each behavior, I define the turning angle frequency with one of two specific von Mises PDFs, $v_0(\theta)$ or $v(\theta|\kappa)$ (Appendix A: Table A.1). I chose the von Mises distribution to be consistent with recent studies comparing Lévy strategy models and the CCRW (Plank et al., 2013; Plank and Codling, 2009). The von Mises distribution has two parameters: α, which is the location parameter and can be interpreted as the mean angle between steps; and κ, which is the scale parameter and can be interpreted as the size of the directional correlation. To represent the intensive search as a Brownian walk, I set $\kappa_{\mathrm{I}} = 0$. This reduces the von Mises distribution to an uniform circular distribution and makes the value of α_{I} irrelevant (Evans et al., 2000). This von Mises distribution is represented as $v_0(\theta)$ (Appendix A: Table A.1). To represent the extensive search as a correlated random walk, I set $\alpha_{\mathrm{E}} = 0$ and estimate κ_{E}. This von Mises distribution is similar to a circular version of the Gaussian distribution centered at 0 (Evans et al., 2000) and is represented as $v(\theta|\kappa)$ (Appendix A: Table A.1).

For each behavior, I define the step length frequency with a slightly modified exponential distribution, $\phi(l|\lambda, a)$ (Appendix A: Table A.1). The exponential distribution was used in previous attempts to compare multiphasic movement to Lévy walk (Jansen et al., 2012; Plank et al., 2013) and defines the probability of a step length as exponentially decreasing with increasing size. My exponential distribution starts at the minimum step length, a, rather than starting at 0. This modification is equivalent to applying the exponential distribution to the difference between the step length and the minimum step length, $l - a$, and makes the CCRW more comparable to the models used for the Lévy strategy (Edwards et al., 2007; Jansen et al., 2012). Each exponential distribution has two parameters to estimate: the minimum step length, a, and the rate parameter, λ. While the minimum step length, a, is assumed to be the same for both behaviors, λ differs between behaviors: λ_{I} and λ_{E}. We can interpret λ as the inverse of the mean step length (Evans et al., 2000), or more precisely as the inverse of the mean difference between step lengths and the minimum step length, $\lambda = n/(\sum_{t=1}^{n} l_t - a)$. Thus a difference between λ_{I} and λ_{E} captures differences in the distances moved in each behavior. By combining the exponential and von Mises distributions, we get the following observation PDFs associated with each behavior:

$$p_{\mathrm{I}}(l_t, \theta_t) = \phi(l_t|\lambda_{\mathrm{I}}, a)\; v_0(\theta_t), \tag{3.1}$$

and

$$p_{\mathrm{E}}(l_t, \theta_t) = \phi(l_t|\lambda_{\mathrm{E}}, a)\; v(\theta_t|\kappa_{\mathrm{E}}). \tag{3.2}$$

The observation PDFs describing the movement of each behavior are combined through what is referred as a mixing distribution. The choice of mixing distribution is an important difference between my model and the previous attempts to compare multiphasic movement to Lévy walk (Jansen et al., 2012; Plank et al., 2013). Previous models combined the observation probabilities through an independent mixing distribution, where the probability of intensively searching, I, and that of extensively searching, E, are independent of previous probabilities and constant through time. Although these models provide good approximations to the movement of an animal that has two behaviors, they do not represent the temporal correlation in behaviors that a hidden Markov model can provide. Behavioral persistence is crucial when modeling the ARS strategy without including environmental variables as the trigger for behavioral switches. In my case, I implicitly represent the spatial correlation that a patchy landscape would create with temporal correlation in behavior. Thus, unlike models with an independent mixing distribution, the order of the observations is important in a hidden Markov model.

I used the methods of Zucchini and MacDonald (2009) to create a hidden Markov model from my observation probabilities. The mixing distribution is a first-order Markovian process, where the probability of being in a behavior at time t, e.g., I_t, depends on the previous time steps probabilities, I_{t-1} and E_{t-1}, and on the transition probability matrix:

$$\mathbf{\Gamma} = \begin{pmatrix} \gamma_{\mathrm{II}} & 1 - \gamma_{\mathrm{II}} \\ 1 - \gamma_{\mathrm{EE}} & \gamma_{\mathrm{EE}} \end{pmatrix}, \tag{3.3}$$

where γ_{II} and γ_{EE} are the probabilities of remaining in the intensive and extensive search behaviors, respectively, and $1 - \gamma_{\mathrm{II}}$ and $1 - \gamma_{\mathrm{EE}}$ are the probabilities of switching from intensive to extensive and from extensive to intensive, respectively. Because the duration of each movement phase follows a geometric distribution, $1/(1 - \gamma_{\mathrm{II}})$ and $1/(1 - \gamma_{\mathrm{EE}})$ can be interpreted as the mean number of steps the animal remains in the intensive and extensive search, respectively. Thus, an animal that remains on average more than two steps in the same search behavior will have γ_{II} and $\gamma_{\mathrm{EE}} > 0.5$. As the probability of being in a behavior depends on the previous probabilities, I need to define the initial probability of being in each behavior:

$$\boldsymbol{\delta} = \begin{pmatrix} \delta_{\mathrm{I}} & 1 - \delta_{\mathrm{I}} \end{pmatrix}, \tag{3.4}$$

where δ_{I} and $1 - \delta_{\mathrm{I}}$ are the probabilities of starting in the intensive and extensive search behaviors, respectively. The likelihood of the CCRW is:

$$L_{\mathrm{CCRW}}(\mathbf{\Theta}|\boldsymbol{l}, \boldsymbol{\theta}) = \boldsymbol{\delta}\boldsymbol{P}(l_1, \theta_1) \prod_{t=2}^{n} (\mathbf{\Gamma}\boldsymbol{P}(l_t, \theta_t))\, \mathbf{1}, \tag{3.5}$$

where $\mathbf{1}$ is a column vector of ones and $\boldsymbol{P}(l_t, \theta_t)$ is the observation probability matrix that incorporates the probability of being in each behavior as defined by Eqns. 3.1 and 3.2:

$$\boldsymbol{P}(l_t, \theta_t) = \begin{pmatrix} p_{\mathrm{I}}(l_t, \theta_t) & 0 \\ 0 & p_{\mathrm{E}}(l_t, \theta_t) \end{pmatrix}. \tag{3.6}$$

The expanded formula of the likelihood can be found in Table 3.1.

To make the likelihood of the Lévy strategy comparable to the CCRW, I used a PDF for the turning angle in addition to the PDF that is generally used to describe the step lengths of the Lévy strategy (Table 3.1). The turning angle of the Lévy strategy is generally assumed to be uniform (Bartumeus et al., 2005; Plank et al., 2013). Thus, I used the same circular uniform PDF, $v_0(\theta)$, as described above (Appendix A: Table A.1). Two step length PDFs can be used to described the Lévy strategy. One represents the pure Lévy walk, the other represents the truncated Lévy walk (TLW). Unlike the pure Lévy walk, the TLW places an upper bound on the size of possible step lengths, making it biologically plausible (Viswanathan et al., 2008). As a result, the TLW is often used as a Lévy strategy model for animal movement (e.g., Sims et al., 2012). The step length PDF of the TLW is the truncated Pareto, $\psi_{\mathrm{T}}(l|\mu_{\mathrm{T}}, a, b)$ (Appendix A: Table A.1). This distribution has three parameters to estimate: the shape parameter, μ_{T}, which increases the probability of long step length as it decreases, the minimum step length, a, and the maximum step length, b, which represents the greatest step length an animal can make. While I focused on the TLW in Chapter 3, I present analyses of the pure Lévy walk in Appendix A.

To verify that the complexity associated with the CCRW and TLW is required to explain the data, it is important to compare these models against simpler ones. Therefore I developed likelihood functions for two simpler models: the truncated Brownian walk (TBW) and the truncated correlated random walk (TCRW; Table 3.1). The TBW is an absolute null model representing an individual moving randomly in space, while the TCRW represents movement with directional persistence. These models are closely related to the null models used in Lévy walk studies (Bartumeus et al., 2005; Edwards et al., 2007). Similar to the observations PDFs of the CCRW (Eqns. 3.1 and 3.2), the likelihoods use the von Mises PDF for the turning angle and the exponential PDF for the step length. To make the models analogous to the TLW, which has an upper bound on the step length size, I used the truncated version of the exponential distribution, $\phi_{\mathrm{T}}(l|\lambda_{\mathrm{T}}, a, b)$ (Edwards et al., 2007) (Appendix A: Table A.1). Analyses of the non-truncated version of these two models are available in Appendix A.

Statistical measures

To assess the support for each search strategy, I used the likelihood functions described above with a set statistical measures. First, I estimated the model parameters and their confidence intervals with maximum likelihood estimate (MLE) and through likelihood surface analyses. Second, I compared the fit of the models with Akaike Information Criterion (AIC) and Akaike weights. Finally, I tested the absolute fit of the models through analyses of pseudo-residuals. I performed these analyses with R 2.15.2 (R Development Core Team, 2012).

I used maximum likelihood to estimate the parameters of the models described above (Table 3.2). I used known analytical solutions for the MLE of a and b (Edwards et al., 2012). For the remaining parameters, I used numerical optimizing functions and, in the case of the CCRW, I used the Expectation-Maximization (EM) algorithm described by Zucchini and MacDonald (2009). I used the EM algorithm for the CCRW because it is orders of magnitude faster than the direct numerical maximization of its likelihood. Given that I fit the CCRW to 633 000 simulations, computational efficiency was an important consideration (see Section 3.2.2). The disadvantage of using the EM algorithm over the direct maximization is the need to estimate δ_{I} (Zucchini and MacDonald, 2009), a parameter with little biological relevance.

To estimate the confidence intervals of the parameters, I used the quadratic approximation described by Bolker (2008). This method uses the Hessian of the negative log likelihood at its minimum value. As the analytical solution of a and b is to use the minimum and maximum observed step lengths (Edwards et al., 2012) and the estimated value from EM algorithm for δ_{I} depends only on the observations of the first step (Zucchini and MacDonald, 2009), it is difficult to estimate confidence interval for these three parameters. I only provide point estimates for them.

The main goal of my likelihood functions is to identify which model fits the data best. To do so, I compared the relative fit of the models using AIC_c and Akaike weights (Burnham and Anderson, 2002). The model with the lowest AIC_c is considered to be the best model. To measure the weight of evidence the best model has over the other models, I calculated Akaike weights, w, from the AIC_c values of the models (Burnham and Anderson, 2002). Akaike weight values vary between 0 and 1, with a weight close t 1 suggesting that the data strongly support this model over the other models investigated.

As the best model according to AIC_c and Akaike weights can still be a poor representation of the data, it is important to verify its absolute fit (Chapter 2). In the context of Lévy walk analyses, the suggested test of absolute fit is a G-test (Edwards, 2011; Edwards et al., 2007), a test that assumes that observations are independent of one another. This assumption is violated in the case of the CCRW because this model incorporates temporal autocorrelation. Hence, I modified the test of absolute fit by applying the G-test to pseudo-residuals rather than to observations. I used ordinary uniform pseudo-residuals, which are residuals that account for the interdependence of observations and are uniformly distributed when the model adequately describes the data (Zucchini and MacDonald, 2009). I performed a G-test that compares the observed frequency of these pseudo-residuals to a discretized uniform distribution. To reduce the potential bias associated with bins that have small expected values, I used William's correction and ensured that each bin had 10 expected pseudo-residuals (Sokal and Rohlf, 1981). I applied the G-test to the pseudo-residuals of step length and turning angle independently and subsequently combined their p-values using Fisher's method (Sokal and Rohlf, 1981). Appendix B describes the test of absolute fit in more detail.

3.2.2 Simulation study

I used simulations of the TLW and CCRW to assess whether my method can differentiate between the Lévy and the ARS strategies. Because parameter values affect the resemblance of these strategies, I simulated the CCRW and TLW on a range of parameter values. For each set of parameters, I ran a 1000 simulations, each creating a movement path of 500 moves. For each simulation, I used my proposed method to estimate the parameter values and calculate the Akaike weights of all models. This allowed me to verify that the method could accurately estimate parameters and appropriately differentiate between models. To assess whether the true model was rejected at the appropriate α-level, I also calculated the p-value of the absolute fit test associated with the simulated model.

To simulate the CCRW, I initialized the movement path by selecting the starting behavior, either I_1 or E_1, using a Bernoulli distribution with probability of being in the intensive search behavior defined by δ_{I}. If the behavior was the intensive search, I randomly selected a turning angle from a circular uniform distribution and a step length from an exponential distribution with λ_{I}. If the behavior was the extensive search, I randomly selected a turning angle from a von Mises distribution with κ_{E} and a step length from an exponential distribution with λ_{E}. After selecting the turning angle and step length for the first step, I selected the next behavioral state with a Bernoulli distribution that used the transition probability appropriate for the current behavior (i.e., γ_{II} if in intensive search and γ_{EE} if in extensive search). As for the first step, I then selected a step length, a turning angle and the behavioral state for the next step from the appropriate distributions. This process was continued until the last step of the movement path. The CCRW has seven parameters (Tables 3.1 and 3.2). I fixed the values of δ_{I}, λ_{I}, and a, to 0.5, 0.01, and 1, respectively. I varied the value of κ_{E} to $(0.5, 1, 5, 10)$, that of λ_{E} to $(0.005, 0.001, 0.0005, 0.0001)$, that of γ_{II} to $(0.6, 0.7, 0.8, 0.9)$, and that of γ_{EE} to $(0.1, 0.2, ..., 0.9)$. By choosing $\lambda_{\text{I}} > \lambda_{\text{E}}$, the step lengths from the extensive search behavior were longer on average than those from the intensive search. I chose the values of γ_{II} to be > 0.5 because the intensive search of the ARS strategy is efficient only if the animal remains multiple moves in a food patch. In contrast, I allowed γ_{EE} to be < 0.5 because an efficient extensive search can be produced in one move. All 576 combinations of these parameters were simulated.

For each step of the TLW simulations, I randomly selected a turning angle from a circular uniform distribution, and a step length from a truncated Pareto distribution. The TLW has three parameters (Tables 3.1 and 3.2). I set $a = 1$ and varied the value of μ_{T} to (1.1, 1.2, ..., 2.9) and b to (100, 1000, 10000). All 57 combinations of these parameters were simulated.

3.2.3 Application to empirical data

To demonstrate its usefulness, I applied my method to the movement path of two polar bears from the Western Hudson Bay, Manitoba, Canada. These two females were captured in September 2010 using the standard immobilization techniques (Stirling et al., 1989) and were collared with Gen IV collars from Telonics (Telonics Inc., Mesa, AZ, U.S.A). The collars were programmed to collect GPS locations at varying frequencies throughout the year. I used data from the month of April 2011, the longest period with high frequency locations (location taken every 30 minutes) and a period where bears search for food (Pilfold et al., 2012; Thiemann et al., 2006). These two bears were on the sea ice during this period.

I applied my method (Section 3.2.1) to the data from each individual separately after estimating biologically relevant steps from the raw GPS data. Multiple techniques can be used to transform locations collected at regular time intervals into a time-series of biologically relevant steps (e.g., Codling and Plank, 2011; Humphries et al., 2013). In part for its ease of use, I used the local turn technique, which creates one step out of all consecutive sampled steps with a turning angle smaller than a threshold angle (see Codling and Plank, 2011). Using these types of techniques can results in misidentifying

CCRW for LW (Codling and Plank, 2011; Plank et al., 2013). However, such misidentification occurs mainly when high threshold angles are used (Codling and Plank, 2011; Plank et al., 2013). I chose a threshold angle of 10°, meaning that any sampled step within the 20° forward sector is interpreted as part of a biologically relevant step. Thus resulting steps are created from movement in the same general direction and the threshold is small enough that it is unlikely to result in misidentification. I applied my method to empirical data to demonstrate how to interpret results and to show the performance of my method with real animal movement paths, which, unlike simulated movement, are complicated by factors such as missing data.

3.3 Results

3.3.1 Simulation results

The Akaike weights could differentiate between the Lévy and the ARS strategies. When the CCRW was simulated, 91.2% of the Akaike weight values of the CCRW exceeded 0.99 and the Akaike weight values of TLW never exceeded 0.01 (Fig. 3.1A). Although the CCRW simulations were never misidentified as a TLW, 3.0% of the summed Akaike weight values of the null models, $w_{\mathrm{TBW}}+w_{\mathrm{TCRW}}$, exceeded 0.5. This occurred only when the step length distribution of the extensive search was relatively close to that of the intensive search, $\lambda_{\mathrm{E}} = 0.005$. In addition, this was generally limited to cases when the tendency to continue in the same direction was relatively low, $\kappa_{\mathrm{E}} \leq 1$. When the TLW was simulated, 96.2% of the Akaike weight values of the TLW exceeded 0.99 (Fig. 3.1B). While 3.8% of the Akaike weight value of the CCRW exceeded 0.01, only 0.3% exceeded 0.5. The frequency of these rare misidentifications increased with increasing μ_{T}. Note that, due to underflow, I was unable to estimate the AIC_c value of the CCRW for 0.3% of the simulations. The Akaike weights results presented above and MLE results below ignore all of the problematic simulations.

In addition to differentiating between the two processes, my method was capable of recovering the parameter values of the CCRW and TLW. As some parameter estimates can help identify whether the data are consistent with the Lévy or the ARS strategies, it is important for my method to adequately estimate their values. The ARS strategy requires the CCRW to have specific values for γ_{II}, λ_{I}, λ_{E}, and κ_{E}. Similarly, μ_{T} of the TLW requires specific values to be consistent with the Lévy strategy. For most parameters of the simulated CCRW and TLW, the median of the estimated values was close to their true value (Figs. 3.2 and 3.3). There were three exceptions. First, the estimated values of the initial probability of being in the intensive search of the

CCRW, δ_{I}, approached either 0 or 1, not 0.5 (Fig. 3.2F). Second, some estimates of the minimum step length, a, were positively biased, and those of maximum step length, b, were negatively biased (Figs. 3.2G and 3.3B-C). Third, similar to the Akaike weights, the estimates of most parameters of the CCRW were less accurate when the movement patterns of the two behaviors were similar. Specifically, the estimates were less reliable when the simulations values of λ_{E} were relatively close to λ_{I}. The estimated values of most parameters were much closer to the true value when simulations with $\lambda_{\text{E}} = 0.005$ were excluded.

Finally, my tests of absolute fit had rejection rates adequate for the selected α-level of 0.05 (p-value < 0.05). The proportion of simulated CCRWs that were rejected from being CCRW was 0.062. Similarly, the proportion of simulated TLWs that were rejected from being TLW was 0.065.

3.3.2 Empirical results

The best model for the two empirical movement paths was the CCRW (Table 3.3). For Bear 2, the Akaike weights indicated that the CCRW was a much better model than the other alternatives. However, the Akaike weight of the CCRW for Bear 1 was only 0.77, with some evidence that the TCRW may have been a more parsimonious description of the movement data (Table 3.3 and Fig. 3.4). While the best model was the CCRW, both movement paths were significantly different from it (Table 3.3). The movement path of Bear 1 was also significantly different from the TCRW ($p < 0.01$). A visual representation of the fit of the models is presented in Fig. 3.4.

To identify whether the movement paths were consistent with the best model, I verified whether the parameter estimates of γ_{II}, λ_{I}, λ_{E}, and κ_{E} were consistent with the ARS strategy. For Bear 2, all parameters were consistent: $\gamma_{\text{II}} > 0.5$, $\lambda_{\text{I}} > \lambda_{\text{E}}$, and $\kappa_{\text{E}} > 0$ (Table 3.2). In contrast, not all parameters for Bear 1 were consistent with the ARS. While $\kappa_{\text{E}} > 0$ as expected for the ARS, $\gamma_{\text{II}} < 0.5$ and the confidence intervals of λ_{I} and λ_{E} overlapped (Table 3.2). These results further suggest that Bear 1 had movement consistent with the TCRW.

3.4 Discussion

Through the analysis of TLW and CCRW simulations, I have demonstrated that my method can differentiate between the Lévy and the ARS strategies. The Akaike weights identified the correct underlying search strategy, except for a few instances. The rare misidentifications between the Lévy and the ARS strategies were primarily limited to TLW simulations with high μ_{T} values. As μ_{T} increases, the probability of very long step lengths decreases and the TLW increasingly resembles more conventional random walks. The tendency for TLW to be mistaken for other processes at high μ_{T} values has been observed previously (Plank and Codling, 2009).

The Akaike weights also distinguished the TLW and CCRW from the two null models. The rare exceptions occurred when both the intensive and extensive search behaviors of the CCRW simulations had similar step length and turning angle distributions. This was not surprising. Other methods developed to distinguish between the two behaviors of the ARS are also less efficient when the movement of these behaviors are similar (Knell and Codling, 2012). When the two behaviors are similar, models describing them as one behavior can be sufficient. The ability of my method to differentiate between the CCRW and the null models would likely increase with sample size.

The simulation analyses also indicated that most parameter estimates of the TLW and CCRW were reliable. The estimates of the important parameters of both models (i.e., γ_{II}, λ_{I}, λ_{E}, κ_{E}, and μ_{T}) were generally reliable and accurate. These are the only parameters that should be used to help identify whether the empirical data support the Lévy or the ARS strategies. No biological interpretation should be based on the probability of starting in the intensive search behavior, δ_{I}. As described by Zucchini and MacDonald (2009), the estimates from the EM algorithm for this parameter approached either 0 or 1. Caution should be taken when interpreting the minimum, a, and maximum, b, step lengths. Even though using the minimum and maximum observed step lengths are the MLEs, and is the suggested method to estimate these values for TLW (Edwards et al., 2012), some of their estimates were biased. One likely explanation, is that 500 steps was too small a sample to accurately estimate these parameters. The estimates of most parameters of the CCRW suffered when the two search behaviors were not substantially different.

I have not assessed the accuracy of the confidence intervals through the simulation study because doing so would have significantly increased computational time. However, I note a few known limitations of the method I used to estimate the confidence intervals of the empirical data set. Because precise methods, such as the likelihood profile, become highly unpractical and computationally demanding when models have more than 2 or 3 parameters to be estimated, Bolker (2008) recommends the use of the quadratic approximation for estimating confidence intervals. Because the CCRW had 7 parameters to be estimated, I chose to use this approximation. However, the quadratic approximation can be inaccurate when the parameter estimated is at the boundary of its parameter space (Zucchini and MacDonald, 2009). In fact, this approximation is symmetric around the MLE, thus might exceed the boundary of parameter space. This occurred for a few of the empirical estimates of the confidence intervals (Table 3.2). With these caveats in mind, I believe that such approximation is sufficient for my analyses.

The simulation results showed that my test of absolute fit was adequate, albeit with observed rejection rates that were marginally greater than the expected rate of 0.05. Thus my test had a slightly higher level of type I error than specified by the α-level. This problem could be associated with the known negative bias in p-values of G-tests when sample size and expected values are small (Sokal and Rohlf, 1981). I have also explored the use of a number of other tests, such as tests of normality on normal pseudo-residuals (see Zucchini and MacDonald, 2009, for description of normal pseudo-residuals). None have outperformed the one presented here.

I have not explored the impact of data sampling and handling on the accuracy of my method. Some sampling procedures, in particular subsampling and the definition of steps by the significant turns, are known to cause Akaike weights to select the LW when CCRWs are simulated (Codling and Plank, 2011; Plank et al., 2013; Plank and Codling, 2009). Although my method is likely to be affected by such procedures, it has features that are known to decrease misidentification errors. In particular, it was shown that including an approximation of the CCRW and tests for the absolute fit mitigates the risks of such errors (Plank et al., 2013). Future work should study how sampling procedures impact the capacity of my method to differentiate between the two strategies.

I demonstrated how to interpret the results of my method by applying it to empirical data. My results suggested that the two bears differed in their movement patterns. For Bear 2, the Akaike weights and parameter estimates suggested that the movement path was better represented by the CCRW and was consistent with the ARS strategy. For Bear 1, the Akaike weigths and parameter estimates suggested that although the CCRW was the best model, the TCRW, a one-behaviour null model, might be sufficient to explain the data. These two bears differed in their reproductive status: Bear 1 was accompanied by a yearling at capture while Bear 2 was accompanied by a cub-of-the-year. Females with cubs-of-the-year are known to move smaller distances and use different sea ice habitats than other females (Amstrup et al., 2000; Stirling et al., 1993). Thus, it is possible that females with cubs-of-the-year used different search strategies than other females and this difference could have resulted in the difference observed between the two bears.

An additional explanation for the difference between these two bears is that the quality of their movement paths differ (Fig. 3.4). The results for Bear 1 demonstrated that my method can handle large amount of missing data. However, as with most analytical methods, missing data can impact biological interpretation. Specifically, reduced sample size likely hinders my method's ability to differentiate between models and between the two behaviours of the CCRW. In addition, missing locations divides the path into smaller steps, which has the potential to impact model fit. Thus, I advise ecologists to be cautious when interpreting results for movement paths with many missing locations.

Finally, the movement path of each bear was significantly different from the best model, indicating that my models might be missing important characteristics of polar bear movement. For example, polar bears are known to move against sea ice drift and ignoring drift can impact interpretation of movement paths (Gaspar et al., 2006; Mauritzen et al., 2003). Thus, an important extension for polar bears might be the inclusion ice drift in search strategy models.

3.4.1 Conclusion

I have developed likelihood functions for models representing the ARS and Lévy strategies that make it possible to directly compare the evidence for these two prominent hypotheses. Unlike recently developed methods, my method uses information from both step lengths and turning angles, and incorporates the temporal autocorrelation inherent in the ARS strategy. My simulation study showed that my method could differentiate between the two strategies. By applying my method to the movement path of two polar bears, I showed that my method can give easily interpretable results and handle complex movement paths. I hope that application of this method to empirical data will further our understanding of the mechanisms used by animals to find resources.

Table 3.1: Likelihood functions and number of parameters to estimates, k, of the four models. The ARS strategy is represented by the CCRW, the Lévy strategy by the TLW, and the two null models by the TBW and TCRW. Table A.1 of Appendix A describes the PDFs, $\phi()$, $\phi_{\mathrm{T}}()$, $v()$, $v_0()$, and $\psi_{\mathrm{T}}()$. Table 3.2 describes the parameters.

Model	Likelihood function	k
CCRW	$\begin{pmatrix} \delta_{\mathrm{I}} & 1-\delta_{\mathrm{I}} \end{pmatrix} \begin{pmatrix} \phi(l_1 \vert \lambda_{\mathrm{I}}, a)\, v_0(\theta_1) & 0 \\ 0 & \phi(l_1 \vert \lambda_{\mathrm{E}}, a)\, v(\theta_1 \vert \kappa_{\mathrm{E}}) \end{pmatrix} \prod_{t=2}^{n} \begin{pmatrix} \gamma_{\mathrm{II}} & 1-\gamma_{\mathrm{II}} \\ 1-\gamma_{\mathrm{EE}} & \gamma_{\mathrm{EE}} \end{pmatrix} \begin{pmatrix} \phi(l_t \vert \lambda_{\mathrm{I}}, a)\, v_0(\theta_t) & 0 \\ 0 & \phi(l_t \vert \lambda_{\mathrm{E}}, a)\, v(\theta_t \vert \kappa_{\mathrm{E}}) \end{pmatrix} \begin{pmatrix} 1 \\ 1 \end{pmatrix}$	7
TLW	$\prod_{t=1}^{n} \psi_{\mathrm{T}}(l_t \vert \mu_{\mathrm{T}}, a, b)\, v_0(\theta_t)$	3
TBW	$\prod_{t=1}^{n} \phi_{\mathrm{T}}(l_t \vert \lambda_{\mathrm{T}}, a, b)\, v_0(\theta_t)$	3
TCRW	$\prod_{t=1}^{n} \phi_{\mathrm{T}}(l_t \vert \lambda_{\mathrm{T}}, a, b)\, v(\theta_t \vert \kappa)$	4

Table 3.2: Description and empirical estimates of the model parameters. The parameter estimates and associated confidence intervals (CIs) are presented for each bear.

Symbol (unit)	Description	Bear 1	Bear 2
a (m)	Minimum step length of all four models	21	2
b (m)	Maximum step length of the TLW, TBW, TCRW	12614	11789
δ_{I}	Probability of starting in the CCRW's intensive search	0	0
γ_{II}	Probability of remaining in the CCRW's intensive search	0.48 † (-0.07-1.02)	0.83 (0.75-0.91)
γ_{EE}	Probability of remaining in the CCRW's extensive search	0.91 † (0.79-1.03)	0.97 (0.95-0.99)
κ	Size of the directional correlation of the TCRW	1.41 (1.17-1.66)	1.21 (1.09-1.32)
κ_{E}	Size of the directional correlation of the CCRW's extensive search	1.74 (1.29-2.19)	1.22 (1.09-1.36)
λ_{T} (m^{-1})	Rate parameter of the exponential distribution of the TBW and TCRW	0.0009 (0.0008-0.0010)	0.0010 (0.0009-0.0010)
λ_{I} (m^{-1})	Rate parameter of the CCRW's intensive search	0.0031 (0.0008-0.0053)	0.0100 (0.0071-0.0129)
λ_{E} (m^{-1})	Rate parameter of the CCRW's extensive search	0.0008 (0.0007-0.0010)	0.0008 (0.0008-0.0009)
μ_{T}	Scale parameter of the truncated Pareto distribution of the TLW	1.00 † (0.93-1.07)	1.00 † (0.97-1.03)

† Because I used the quadratic approximation to estimate CIs, some CIs exceed the boundary of their parameter space (see Section 3.4 for details).

Table 3.3: Relative and absolute fit of the four models on the movement paths of two polar bears. For each bear, the ΔAIC_c and Akaike weight for each model, the p-value for the test of absolute fit of the best model according to AIC_c, and the number of steps of the movement are presented.

Individual	n	ΔAIC_c				Akaike weight				p-value
		CCRW	TLW	TBW	TCRW	CCRW	TLW	TBW	TCRW	Best model
Bear 1	235	0	302	172	2	0.77	< 0.01	< 0.01	0.23	< 0.01
Bear 2	887	0	1480	651	139	1.00	< 0.01	< 0.01	< 0.01	< 0.01

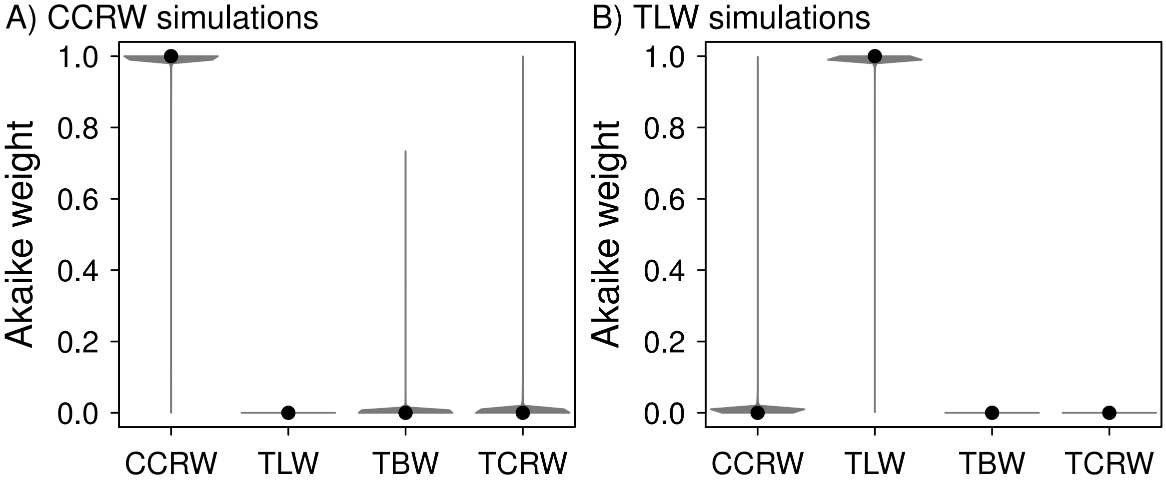

Figure 3.1: Violin plots of the Akaike weights of each model for all simulated CCRWs and TLWs. High Akaike weight values represent strong support for a model relative to the other models. Violin plots are combinations of kernel density plots (gray polygon) and box plots. Because the range of most model values was orders of magnitude smaller than the y-axis, the box plots are only represented by the • symbols that identify the median. Panel A shows that for simulated CCRWs mostly CCRW had strong support. Panel B shows that for simulated TLWs mostly the TLW had strong support.

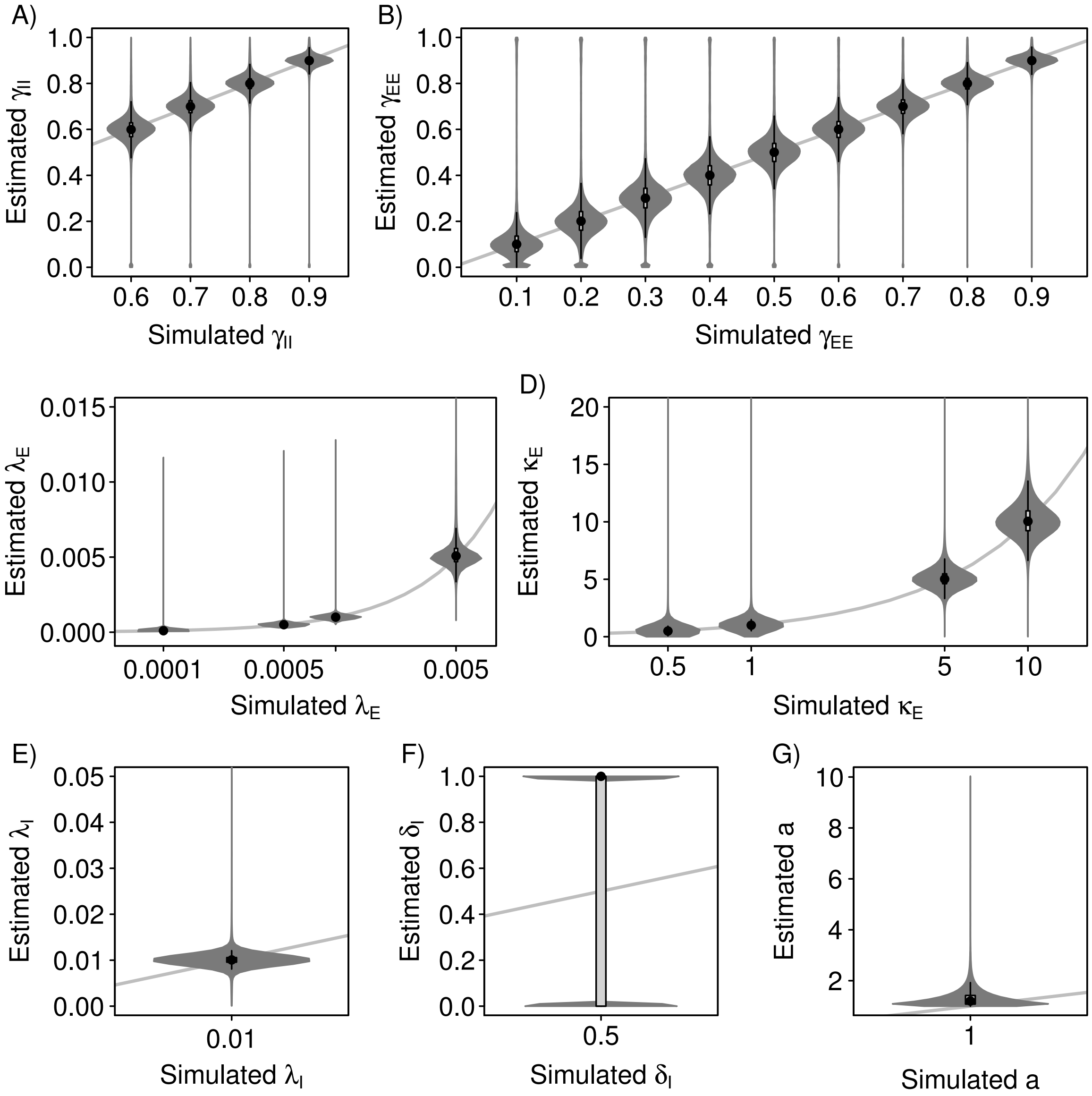

Figure 3.2: Violin plots of the MLE values for the CCRW simulations. The x- and y-axis represent respectively the values used in the simulations and those recovered by MLE. The gray line shows their one-to-one relationship. (A) Probability of remaining in intensive search. (B) Probability of remaining in extensive search. (C) Rate parameter of extensive search. (D) Directional correlation of extensive search. (E) Rate parameter of intensive search. (F) Probability of starting in intensive search. (G) Minimum step length. For visualization, I have cropped out extreme outliers from the plots of λ_{I}, λ_{E}, and κ_{E}, but I removed < 0.7% of results per parameter value.

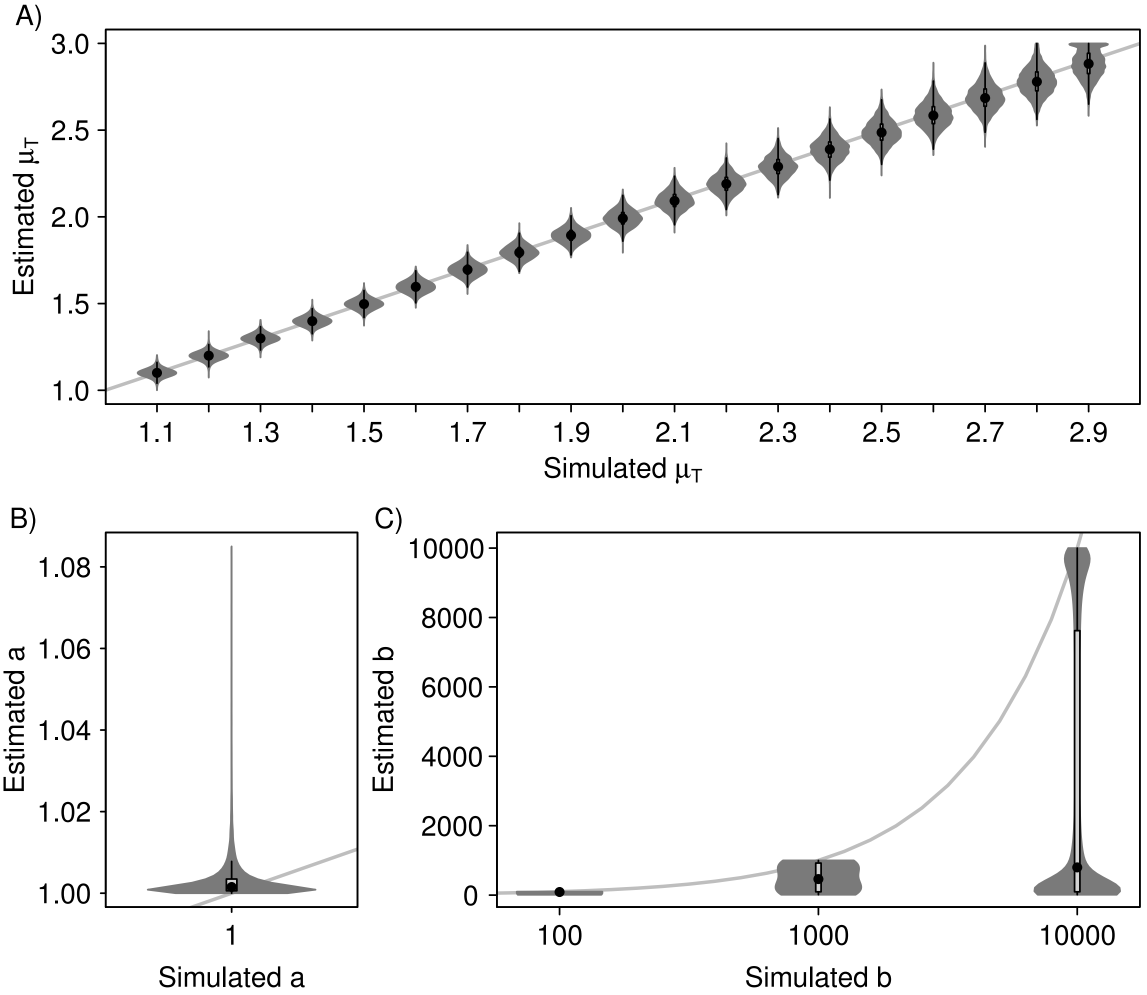

Figure 3.3: Violin plots of the MLE values of the TLW simulations. The x- and y-axis represent respectively the values used in the simulations and those recovered by MLE. The gray line represents their one-to-one relationship. (A) Scale parameter of the truncated Pareto. (B) Minimum step length. (C) Maximum step length. Estimated values of μ_{T} are restricted between 1 and 3.

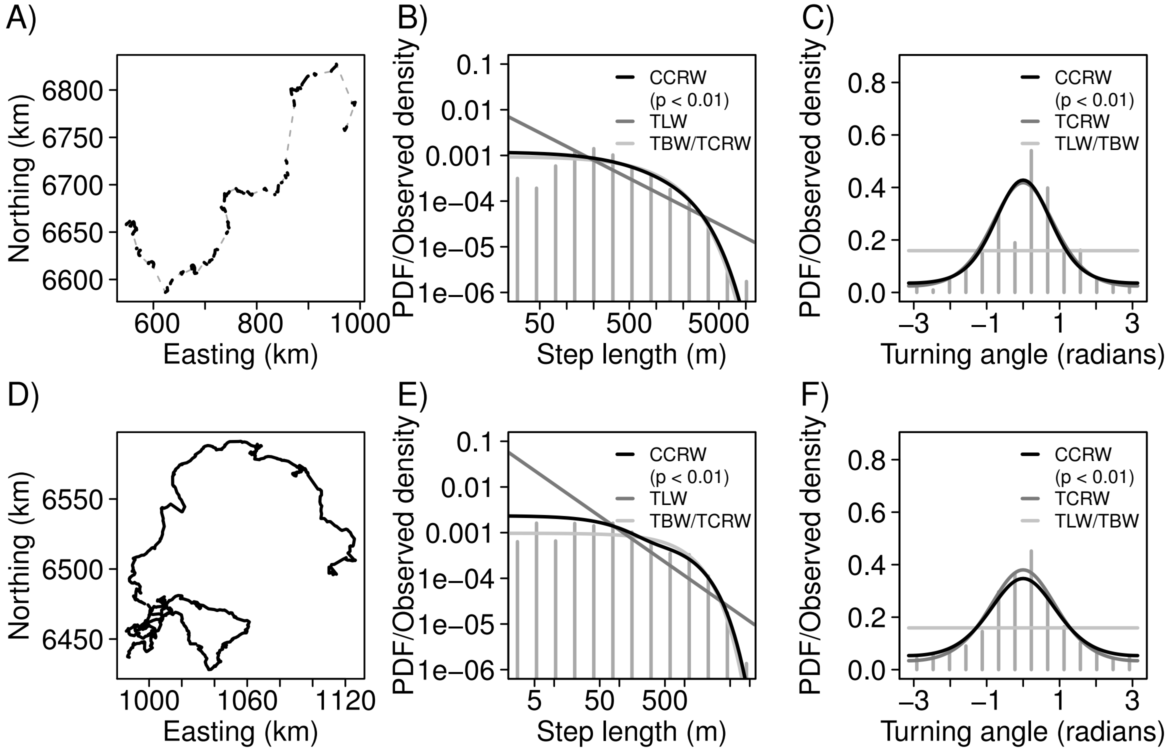

Figure 3.4: Fit of the models to the movement paths of two polar bears. Panels A-C show the results for Bear 1. Panels D-F show the results for Bear 2. (A & D) Movement path, with black lines representing the steps and the dotted line the missing data. (B & E) Step length frequency with the PDF of each model, on log-log axes. (C & F) Turning angle frequency with the PDF of each model. 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.

Chapter 4

Evaluating the evidence for random search strategies in three mammals from distinct feeding guilds

4.1 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 minimize the costs of locating resources (Conradt et al., 2003; Zollner and Lima, 1999). 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 and Tveraa, 2003; Humphries et al., 2010; Nevitt et al., 2008). 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 (Bartumeus et al., 2002; Benhamou, 2007; Plank and Codling, 2009; Zollner and Lima, 1999).

The efficacy of movement strategies are dependent on the variability and predictability of resources distributions (Mueller and Fagan, 2008). When resources are unpredictable in space and time, random search strategies are expected to emerge. 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 but extremely long steps enable animals to explore new areas (Bartumeus et al., 2002; Humphries et al., 2010). Relative to Brownian motion, this prominent search strategy is increasingly efficient with decreasing food density (Bartumeus et al., 2002; Viswanathan et al., 1999). 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 characterized by nearly straight movement that was shown to be efficient at finding sparsely distributed patches (Zollner and Lima, 1999). The area-restricted search (ARS) is a two-behaviour strategy that is more efficient than single-behaviour models in heterogeneous landscape (Benhamou, 1992; Knoppien and Reddingius, 1985; Plank and James, 2008). This prominent strategy combines the nearly straight movement that makes the correlated random walk efficient at finding patches with slower, more tortuous movement once a food item is discovered. The first behaviour is referred as the extensive search, while the second as the intensive search. These two behaviours allow animals to adjust their movement according to local food density and the intensive search enables them to stay within patches, even when patches have no perceptible boundaries (Benhamou, 1992; Knoppien and Reddingius, 1985). Many environments are sparse, heterogeneous, and unpredictable. While Brownian motion and correlated random walk might not be sufficient in these instances, both the Lévy and ARS may be advantageous random search strategies.

The movement patterns of the Lévy and ARS are similar and difficult to differentiate (Benhamou, 2007; Plank and Codling, 2009). In recent years, new methods have been developed to distinguish between these strategies (Plank et al., 2013, Chapter 3). It is now possible to simultaneously assess the evidence for the Lévy and the ARS, as well as the simpler Brownian motion and correlated random walk (Chapter 3). In this Chapter, I investigate the movement of three mammals for evidence of random search strategies. These species vary widely in the foraging behaviours, with each of them belonging to a different feeding guild. However, previous evidence or the nature of their environment suggests that they may use random search strategies.

My first study species is a large herbivore, the woodland caribou (*Rangifer tarandus caribou*). I study them in winter, when resources are scarce (Adamczewski et al., 1987; Parker et al., 2005), and thus, they may be more likely to use random search strategies.

Previous research has indicated that their movement is consistent with a two-behaviour model similar to the ARS and a different subspecies has been suggested to use the Lévy strategy (Johnson et al., 2002*b*; Mårell et al., 2002). Thus applying these newly available tools may help us better identify which of these strategies caribou use.

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

My third species, the polar bear (*U. maritimus*), is a specialized 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). Polar bears exhibit site fidelity (Mauritzen et al., 2001). However, this is also true for the central foragers that have been shown to display random search strategies (e.g., Humphries et al., 2012). Polar bears use the sea ice as a platform to hunt seals (Stirling and Derocher, 2012). Sea ice extent changes seasonally and local ice concentration can vary drastically over short time scales (Johannessen et al., 2004; Maslanik and Barry, 1989), which may make random search strategies advantageous for these bears despite annual site fidelity.

Using movement data collected when these three species are expected to be searching for food, I investigate the support for the use of four random search strategies. I show that for these species there is more evidence for the ARS than for the Lévy walk, Brownian motion, and correlated random walk. The ARS and Brownian motion were sufficient to explain the movement of some individuals, but none of the strategies were adequate for many others. My results demonstrate how species and individuals vary in their searching behaviours, and highlight a need for the development of new strategies.

4.2 Methods

4.2.1 Modeling search strategies

I used the method described in Chapter 3 to assess the support for the search strategies in the movement data of the three species. This method provides a likelihood function for each of the four search strategies (Table 4.1). Each likelihood function was applied simultaneously to the time series of step lengths, l_t and turning angles θ_t. The movement of the Brownian motion was represented with by a truncated Brownian walk (TBW), which uses a modified truncated exponential distribution for the step length, $\phi_{\text{T}}(l)$, and a circular uniform distribution for the turning angle, $v_0(\theta)$ (Table 4.2). The correlated random walk was represented by a truncated correlated random walk (TCRW), which uses a modified truncated exponential distribution for the step length, $\phi_{\text{T}}(l)$, and a von Mises distribution centered at 0 for the turning angle, $v(\theta)$ (Table 4.2). The ARS was represented by a combined correlated random walk (CCRW), which uses a hidden Markov model with two searching behaviours (Table 4.1). The intensive search was represented by a Brownian walk with a modified exponential distribution for the step length, $\phi(l)$, and a circular uniform distribution for the turning angle, $v_0(\theta)$ (Table 4.2). The extensive search was represented by a correlated random walk with a modified exponential distribution for the step length, $\phi(l)$, and a von Mises distribution centered at 0 for the turning angle, $v(\theta)$ (Table 4.2). The Lévy strategy was represented by a truncated Lévy walk (TLW), which uses a truncated Pareto distribution for the step length, $\psi_{\text{T}}(l)$, and a circular uniform distribution for the turning angle, $v_0(\theta)$ (Table 4.2).

To identify the model that best fit the movement data of each individual, the relative fit of these likelihood functions was assessed using AIC_c and Akaike weights (Burnham and Anderson, 2002). I evaluated whether the best model adequately explained the movement data using a test of absolute fit, which comprises of a G-test on uniform pseudo-residuals (Sokal and Rohlf, 1981; Zucchini and MacDonald, 2009). The CCRW and TLW need to have specific parameter values to be consistent with the ARS and Lévy strategies. Thus parameter estimates can serve as additional measures to identify whether the data are consistent with these strategies. I used Maximum Likelihood Estimation (MLE) to estimate the parameters of each model and a quadratic approximation to estimate their confidence intervals (Bolker, 2008). See Chapter 3 for further details.

4.2.2 Description of movement data

To capture rare events, such as the long steps characteristic of the Lévy strategy, I attempted to get time series representing close to a year of searching behavior. However, I also tried to limit the time series to movement performed while searching. As detailed below, I removed all sections of the datasets known to be associated with reproduction and resting, as such behaviour can impact animal movement (e.g., DeMars et al., 2013). I 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.

First, I used 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 GPS locations. I removed the calving and the 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 and Elkie, 2004). Next, I used 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, I used one year of data from July 1st until 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. Finally, I used 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, I started the time series June 1st. I used one year of data. As some pregnant females of the Beaufort Sea give birth in dens on the moving sea ice (Amstrup and Gardner, 1994), it is difficult to identify den location. To exclude denning individuals, I 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 Global Positioning System (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 and Haydon, 2010), and various methods have been proposed (e.g., Codling and Plank, 2011). I 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 and Plank, 2011). It has been shown that this technique, as well as other similar methods, can cause the misidentification of the CCRW for the LW (Codling and Plank, 2011; Plank et al., 2013). However, misidentifications are more likely to occur when high threshold angles are used (Codling and Plank, 2011; Plank et al., 2013). In part to limit the potential for misidentification, I chose a threshold angle of 10°. This threshold angle was also chosen because a biologically relevant step should be defined by movement in the same general direction. With this threshold, any sampled step within the 20° forward sector is interpreted as part of a biologically relevant step. Because the choice of threshold angles can be somewhat arbitrary, I have also explored a range of threshold angles and fit the models to the raw data. I show in Appendix C that the results are broadly similar regardless of the threshold angle used. Note that this method can impact the test of absolute fit (Appendices B and C), and I present only the test of absolute fit for the step length distribution in the main text of this Chapter. Because missing locations can affect the identification of biologically relevant steps, I included only individuals that had a time series with < 30% of the locations missing. I also limited the time series to those with a minimum of 50 steps (Appendix C: Fig. C.3 presents the range of sample size). I applied the models to the data from each individual separately.

4.3 Results

According to AIC_c, the CCRW was the best model for more than 98% of all movement paths and for at least 95% of the movement paths of each species (Table 4.3). For all species, the mean Akaike weight of paths with the CCRW as best model was > 0.92. According to the test of absolute fit, many of the movement paths best described by the CCRW were not significantly different from it: 43% of caribou, 25% of grizzly bears, and 0% of polar bears. For a visual representation of the fit of the models under both step definitions see Fig. 4.1. While the TLW and TCRW were never the best model of a movement path, the TBW was the best model for one of the 22 movement paths of the caribou. The Akaike weight of this TBW was 0.61 and this path was not significantly different from the TBW.

For comparative purposes, I also present the results when only the TLW and TBW are considered as alternative hypotheses. Both models 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 identify the Lévy strategy. The TLW was better than the TBW for almost half of the grizzly bears (9/20) and one polar bear (1/12). The rest of the movement paths, including all caribou paths, were better described by the TBW. While the TBW was sufficient to explain the movement of 11 caribou, it was not sufficient for any of the grizzly or polar bears. All movement paths were significantly different from the TLW.

Many of the parameter estimates of the CCRW were consistent with the expectations of the ARS strategy (Table 4.4). First, the step lengths of the intensive search are expected to be shorter than those of the extensive search behavior. This was the case for all species, as the mean λ_{I} were greater than the mean λ_{E} and their confidence intervals did not overlap. Second, the extensive search movement is expected to be more directed than the intensive search movement. This was the case for the grizzly and polar bears, as the mean κ_{E} and confidence intervals were > 0. However, I had weaker support for caribou, for which the mean κ_{E} was > 0, but not the lower bound of its confidence interval. Third, the intensive search is expected to exhibit behavioural persistence. This was the case for polar bears and caribou, for which the mean transition probabilities, γ_{II}, and their confidence intervals were > 0.5. However, I had weaker support for the grizzly bears. Although the upper bound of confidence intervals was > 0.5, their mean $\gamma_{\mathrm{II}} = 0.46$.

4.4 Discussion

I found substantial support for the CCRW model, and thus the ARS strategy. The CCRW was the best model for 98% of the movement paths, and provided an adequate fit to 26% of them. Moreover, many of the estimated parameters from the CCRW were consistent with the ARS strategy. As expected, the extensive search had higher mean step length and directional persistence than the intensive search. In addition, some animals exhibited behavioral persistence characteristic of the intensive search. However, not all movement paths were consistent with the ARS. The movement paths of many caribou, grizzly bears, and all polar bears were significantly different from the CCRW. In addition, the confidence intervals on some parameter estimates indicated that the evidence for directed movement and behavioral persistence was not strong for some species. These discrepancies indicate that although the CCRW can approximate the movement better than the three other models investigated, it might not completely represent the search strategy of the animals studied.

I found little support for the Lévy strategy. No movement path had the TLW as its best model (although one movement did when using high threshold angle, see Appendix C). The lack evidence for the Lévy strategy is consistent with recent studies, which indicate that the Lévy strategy may not be as common as originally thought (Edwards et al., 2012, 2007; James et al., 2011, but see Humphries et al. 2012; Sims et al. 2012). Although I found little support for the Lévy strategy when all models were considered, support for it increased when the CCRW was excluded from the set of alternative models. When the TLW was compared only to the TBW, close to half of the grizzly bears and one polar bear had the TLW as their best model. This re-emphasizes the importance of comparing the Lévy search strategy to strong alternative models such as the CCRW (Chapter 2; Jansen et al., 2012; Plank et al., 2013). It also supports the contention that some Lévy walk movement patterns might emerge from intermittent movement, rather than providing evidence for the Lévy strategy per se (Benhamou, 2007; Plank and James, 2008). Finally, the fact that all empirical movement paths differed significantly from the TLW further indicates that it was an inappropriate model for my data. This reiterates the importance of testing the absolute fit of a model (Chapter 2; Plank et al., 2013).

The fact that I found support for the CCRW is not surprising given that there is ample evidence of species showing similar biphasic movement behavior (e.g. Dragon et al., 2012; Jonsen et al., 2007; Morales et al., 2004), including evidence for such behavior in caribou (Johnson et al., 2002*a*,*b*; Tyson et al., 2011). However, my results contrast with previous research on semi-domesticated reindeer (*R. t. tarandus*), an Eurasian subspecies of caribou. The movement of reindeer in spring and early summer was more consistent with the Lévy strategy than with null models (Edwards, 2011; Mårell et al., 2002). This was not the case with the winter movement of my caribou. The TBW was a better model than the TLW for all individuals. While I found support for the CCRW, reindeer showed no evidence of increased ARS movement behaviour with increased food density (Mårell et al., 2002). One reason for these apparent differences may be that the movement of many caribou is well explained by the CCRW but is not consistent with the ARS strategy. The ARS strategy assumes that the intensive search behavior is triggered by the encounter of a food item and associated with food patches (Benhamou, 1992). Many studies have indicated that movement consistent with the intensive search are not always associated with food encounters or other foraging proxies (Robinson et al., 2007; Thums et al., 2011; Weimerskirch et al., 2007). However, these differences might also be due to behavioural variation between subspecies or between wild and domesticated animals. They may also results from differences in the sampling scale, habitat, and season examined in the studies. Mårell et al. (2002) showed that reindeer changed their movement strategies over the course of the summer. For caribou, Johnson et al. (2002*a*) 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 use ARS in the winter but not during the summer.

Unlike the grizzly and polar bears, some caribou had the TBW as their best model. In addition, many of the caribou movement paths were not significantly different from the TBW and the parameter estimates indicate that the distinction between the two behaviors of the CCRW were not strong. The caribou movement paths had the smallest sample sizes (see Fig. C.3 in Appendix C). This may have favoured finding evidence for a simpler model in this species, and might have contributed to the relatively low rate of rejection for caribou. However, Edwards (2011) also found that null models similar to the TBW were sufficient to explain reindeer movement in late summer, supporting my results that the TBW is sufficient to explain the movement of some caribou in winter.

The CCRW was the best model for all grizzly bears and was sufficient to explain the movement paths of many individuals. Evidence for a random search strategy, such as the ARS, was anticipated because the bears in this population inhabit sparse and unpredictable environments and display home range drift (Edwards et al., 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 shown to be 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 the CCRW. We might expect the ARS strategy to be more effective for the herbivorous bears exploiting vegetation patches than for canivores preying on large herd animals. Further research could investigate how difference in diet are reflected in the search strategies used by grizzly bears.

The CCRW was the best model for all polar bears, but was insufficient to explain their movement. The parameter estimates indicate that there is a strong differentiation in both step length and directional persistence between the behaviours. Thus, while the movement is not consistent with the ARS strategy, this suggests that polar bear have two movement modes. Difference in these modes could be driven by a variety of factors, including alterations in movement according to sea ice condition. As polar bears adjust their movement to compensate for sea ice drift (Mauritzen et al., 2003), neglecting sea ice drift may partially explain why my models were insufficient to explain their movement. Although previous studies have found evidence for random search strategies in animals experiencing drift from ocean and wind currents (e.g., Fauchald and Tveraa, 2003; Humphries et al., 2012; Sims et al., 2012), it has been shown that 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 four strategies failed to accurately represent many 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 modeled by our idealized representation of search strategies, and with large sample sizes, any small deviation could result in rejection. In particular, there are many ways in which the ARS strategy could be modeled and certain changes to the CCRW could increase its absolute fit. My CCRW used specific distributions for the frequency of step lengths and turning angles. The choice of such distributions can affect the movement behavior of random walks (Codling et al., 2010) and other distributions have been used in some multiphasic movement models (e.g., Langrock et al., 2012; Morales et al., 2004). While my choices were made to reduce the number of parameters to be estimated or to ensure that certain characteristics of the ARS were respected, other choices might increase the absolute fit of the CCRW. Second, it is unlikely that I have sampled the movement paths at the exact scale at which the animals are making their decisions. Sampling scale affects behavioral inference made from movement data (e.g., Andersen et al., 2008; Codling and Hill, 2005; Plank and Codling, 2009). Thus, a lack of strong evidence for the Lévy and ARS strategies at the scale at which I have sampled my movement paths does not preclude the possibility for such evidence at different scales. Further studies that investigate the evidence for movement strategies at multiple scales should be performed (e.g., Fryxell et al., 2008; Gautestad, 2013). Third, although the models are good representations of a movement path composed of biologically relevant moves, they are not necessarily good representations of observed movement. I used a method to estimates biologically relevant moves, but these methods can distort movement paths (Codling and Plank, 2011; Plank et al., 2013). Thus, although I found consistent results over a range of threshold angles (see Appendix C), it may be beneficial to develop a new class of models that directly represent the impact of data handling on the observed movement paths.

In addition to these methodological reasons, there are at least four potential biological reasons for the lack of fit of the two search strategies. First, the Lévy and ARS strategies were developed for animals with scant knowledge of their environment (James et al., 2011; Knoppien and Reddingius, 1985). Species like the caribou and polar bear have been shown to exhibit some degree of site fidelity (Faille et al., 2010; Mauritzen et al., 2001; 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, and evidence for, memory-based movement models (Börger et al., 2008; Fagan et al., 2013; Smouse et al., 2010). Memory-based search strategy can be more efficient than random search strategy (Benhamou, 1994) and may provide better representations of the search strategies used by animals with knowledge of their environment. Second, the Lévy and ARS strategies were developed for animal searching outside of their perceptual range (Benhamou, 1992; James et al., 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 (Conover, 2007; Stirling, 1999), as well as species that have been suggested to follow a random search strategy (e.g., the wandering albatrosses (*Diomedea exulans*), Humphries et al., 2012; Nevitt et al., 2008). As with knowledge of the environment, the ability to use olfactory cues is likely to make other search strategies optimal. Third, landscape features can alter animal movement patterns and affect their search strategy. Including these features into movement models can enhance our understanding of animals' foraging success (McKenzie et al., 2012). Fourth, animals have an extensive behavioral repertoire and their movement paths often include behaviors other than searching for food. Neglecting to remove other behaviors has been shown to distort analysis of search strategies (Edwards et al., 2007). I removed two types of resting periods, the denning period of bears and all steps where locations remained constant. In addition, I removed the main reproductive and mating periods of all species. However, given that my sampling interval was coarse and that the movement paths encompassed months, it is likely that many behaviors, including nursing, predator avoidance, and socializing, are still present in the movement paths. These four explanations for the lack of fit of simple search strategies emphasizes how difficult it is to understand how animal search for food, and echoes recent calls for more mechanistic movement models (Nathan et al., 2008; Schick et al., 2008).

While I have found evidence for the ARS and Brownian movement, 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, perceptual capacities, currents, landscape features, as well as the scale at which the animal search for food and the impact of sampling on observed movement paths.

Table 4.1: Likelihood functions and number of parameters to estimates, k, of the four models. The ARS strategy is represented by the CCRW, the Lévy strategy by the TLW, the Brownian motion by the TBW, and the correlated random walk by the TCRW. Table 4.2 describes the probability density functions, $\phi()$, $\phi_{\mathrm{T}}()$, $v()$, $v_0()$, and $\psi_{\mathrm{T}}()$.

Model	Likelihood function	k
CCRW	$\begin{pmatrix} \delta_{\mathrm{I}} & 1-\delta_{\mathrm{I}} \end{pmatrix} \begin{pmatrix} \phi(l_1 \mid \lambda_{\mathrm{I}},a)\, v_0(\theta_1) & 0 \\ 0 & \phi(l_1 \mid \lambda_{\mathrm{E}},a)\, v(\theta_1 \mid \kappa_{\mathrm{E}}) \end{pmatrix} \prod_{t=2}^{n} \begin{pmatrix} \gamma_{\mathrm{II}} & 1-\gamma_{\mathrm{II}} \\ 1-\gamma_{\mathrm{EE}} & \gamma_{\mathrm{EE}} \end{pmatrix} \begin{pmatrix} \phi(l_t \mid \lambda_{\mathrm{I}},a)\, v_0(\theta_t) & 0 \\ 0 & \phi(l_t \mid \lambda_{\mathrm{E}},a)\, v(\theta_t \mid \kappa_{\mathrm{E}}) \end{pmatrix} \begin{pmatrix} 1 \\ 1 \end{pmatrix}$	7
TLW	$\prod_{t=1}^{n} \psi_{\mathrm{T}}(l_t \mid \mu_{\mathrm{T}}, a, b)\, v_0(\theta_t)$	3
TBW	$\prod_{t=1}^{n} \phi_{\mathrm{T}}(l_t \mid \lambda_{\mathrm{T}}, a, b)\, v_0(\theta_t)$	3
TCRW	$\prod_{t=1}^{n} \phi_{\mathrm{T}}(l_t \mid \lambda_{\mathrm{T}}, a, b)\, v(\theta_t \mid \kappa)$	4

Table 4.2: 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.

Symbol	PDF	Restrictions
$\phi(l \mid \lambda, a)$	$\lambda\, e^{-\lambda(l-a)}$	$a \leq l, \quad \lambda > 0$
$\phi_{\mathrm{T}}(l \mid \lambda_{\mathrm{T}}, a, b)$	$\frac{\lambda_{\mathrm{T}}\, e^{-\lambda_{\mathrm{T}} l}}{e^{-\lambda_{\mathrm{T}} a} - e^{-\lambda_{\mathrm{T}} b}}$	$a \leq l \leq b, \quad \lambda > 0$
$\psi_{\mathrm{T}}(l \mid \mu_{\mathrm{T}}, a, b)$	$\frac{(\mu_{\mathrm{T}}-1)\, l^{-\mu_{\mathrm{T}}}}{a^{1-\mu_{\mathrm{T}}} - b^{1-\mu_{\mathrm{T}}}}$	$a \leq l \leq b, \quad 1 < \mu \leq 3$ †
$v(\theta \mid \kappa)$	$\frac{1}{\int_{-\pi}^{\pi} e^{\kappa \cos(\theta)}\, d\theta} e^{\kappa \cos(\theta)}$ ‡	$\kappa > 0$
$v_0(\theta)$	$\frac{1}{2\pi}$	

† Although the truncated Pareto distribution allow for a greater range of values for μ_{T}, I am restricting its values to those relevant to the Lévy strategy.

‡ 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.

Table 4.3: Relative and absolute fit of the four models on the movement paths of 20 grizzly bears, 12 polar bears, and 22 caribou. For each model, I present the number of movement paths selected as best model with AIC_c and the mean Akaike weight, w, of these selected paths. I also present how many of the selected paths are not significantly different from this 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	21	20	12	0.92	1.00	1.00	9	5	0
TLW	0	0	0	–	–	–	–	–	–
TBW	1	0	0	0.61	–	–	1	–	–
TCRW	0	0	0	–	–	–	–	–	–

Table 4.4: 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 (m)	Minimum step length of the TBW and CCRW	53	3	23
b (m)	Maximum step length of the TBW	15056	–	–
γ_{II}	Probability of remaining in the CCRW's intensive search	0.98 [†] (0.94-1.01)	0.46 (0.34-0.58)	0.84 (0.75-0.92)
γ_{EE}	Probability of remaining in the CCRW's extensive search	0.92 [†] (0.80-1.05)	0.86 (0.79-0.92)	0.96 (0.93-0.99)
κ_{E}	Size of the directional correlation of the CCRW's extensive search	0.25 [†] (-0.23-0.74)	0.41 (0.20-0.62)	1.20 (0.97-1.44)
λ_{T} (m^{-1})	Rate parameter of the exponential distribution of the TBW	0.00055 (0.00043-0.00066)	–	–
λ_{I} (m^{-1})	Rate parameter of the CCRW's intensive search	0.00076 (0.00053-0.0098)	0.06002 (0.02946-0.09057)	0.01607 (0.01247-0.01967)
λ_{E} (m^{-1})	Rate parameter of the CCRW's extensive search	0.00035 (0.00022-0.00048)	0.00056 (0.00048-0.00064)	0.00019 (0.00018-0.00021)

[†] Because I used the quadratic approximation to estimate CIs, some CIs exceed the boundary of parameter space (see Chapter 3 for details).

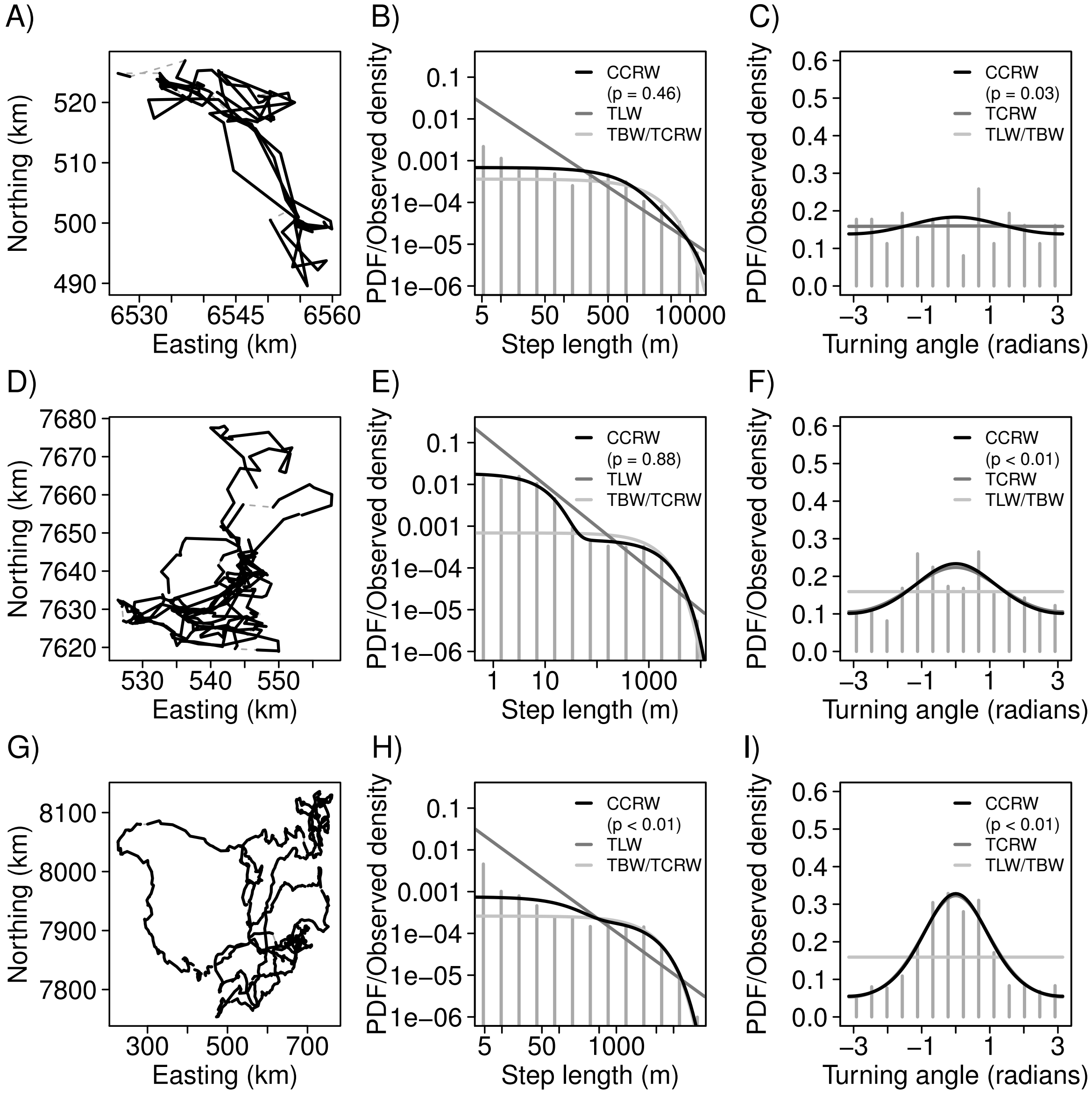

Figure 4.1: Fit of the models to the movement path of each species: (A-C) caribou, (D-F) grizzly, and (G-I) polar bear. In Panels A, D, & G, the black lines represent the movement path using the 10° threshold angle and the gray dashed line the missing data. Panels B, E, & H display the step length frequency with the probability density function (PDF) of each model, on log-log axes. Panels C, F, & I displays the turning angle frequency with the PDF of each model. The best model for these three individuals was the CCRW with $w_{CCRW} > 0.99$. 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.

Chapter 5

Home ranges in moving habitats: polar bears and sea ice

5.1 Introduction

The formation of a home range is a ubiquitous space use behaviour that affects many of the fundamental ecological processes influencing the abundance and distribution of organisms (Börger et al., 2008). As such, the concept of home range has become an important part of ecological research and wildlife management. Burt (1943) formalised the definition of home range as the "area traversed by the individual in its normal activities of food gathering, mating, and caring for young". Although this basic definition is imprecise (Cooper, 1978; White and Garrott, 1990), two notions emerge as central to the home range concept. First, home ranges are associated with site fidelity and an animal's familiarity with an area (Cooper, 1978; Powell and Mitchell, 2012; Spencer et al., 1990). This familiarity may provide knowledge that confers fitness benefits (Powell and Mitchell, 2012). Consequently, there has been increased interest in the importance of memory and cognitive maps in the formation of home ranges (e.g., Powell and Mitchell, 2012; Van Moorter et al., 2009). Second, home ranges have long been used to represent the amount of space required by animals to acquire the resources necessary for their survival and reproduction (e.g., Kelt and Van Vuren, 1999; McNab, 1963; Reiss, 1988). This aspect of home ranges is at the heart of studies that explain variation in home range size across species or individuals (e.g., Kelt and Van Vuren, 1999; McNab, 1963; Tufto et al., 1996). It is also central to studies assessing optimal home range dimensions in terms of the costs and benefits of reaching spatially distributed resources (e.g., Mitchell and Powell, 2004, 2007), and those that seek to identify important habitats (e.g., Edwards et al., 2013; Millspaugh et al., 2006; Tufto et al., 1996).

These two central aspects of home ranges are spatially linked for terrestrial species, and can be assessed simultaneously using statistical tools such as the kernel-based utilisation distribution (Worton, 1989). By delineating the geographic area repeatedly visited by an individual, these statistical tools also capture the amount of habitat used by the animal to gather resources. However, for many species that live in drifting habitats (e.g., oceans, rivers, sea ice, and the atmosphere), the direct spatial link between the geographic area and resources encountered is lost. If resources are drifting in and out of a geographic area, the area cannot be assigned the fixed habitat quality needed to easily relate its size to the amount of resources it provides. The amount of resources encountered in a given location will depend on the strength of currents and the productivity in the area from which the current emerge. Thus, the amount of resources provided by the same geographic area could vary widely through time. In addition, the movement direction of an animal in relation to the drift direction will impact the costs and benefits of space use. First, whether an animal is passively drifting with the current or actively moving against the flow will influence the amount of resources encountered. Second, because moving with or against current significantly impacts the energy expenditure of an animal (Gaspar et al., 2006), we can no longer use distance moved as a proxy for the energetic cost of reaching a food patch.

Here, I provide a first attempt to incorporate drift in home range analyses and demonstrate the potential benefits of this approach. I use polar bears (*Ursus maritimus*) as my study species, as their interaction with the two-dimensional sea ice platform provides a relatively simple illustration of the challenges associated with studying home ranges in drifting habitats. Polar bears hunt seals on the sea ice, and many bears spend a significant part of the year on drifting pack ice (Amstrup et al., 2000; Mauritzen et al., 2003; Stirling et al., 1993). Sea ice can move many kilometres per day (e.g., Hakkinen et al., 2008). Individual polar bears tracked for multiple years return to the same location to forage in the spring and recreate similar movement patterns yearly (Amstrup et al., 2000; Born et al., 1997; Mauritzen et al., 2001). Thus, the geographic area used by bears corresponds to the site fidelity aspect of their home range. However, resource-linked aspects, such as the amount of sea ice visited, the amount prey encountered, and the energy they expend cannot be related to this geographic area without incorporating ice drift. This is particularly important for polar bears because the distribution of their main prey, the ringed seal (*Pusa hispida*), is linked to the sea ice. Ringed seals must maintain breathing holes and lairs to prevent them from freezing closed from freeze-up to melting, and thus are tied to a specific piece of ice for much of the year (Kelly et al., 2010; Smith and Stirling, 1975). Many ringed seals choose stable landfast ice to construct their lairs, but others inhabit drifting pack ice (Kelly et al., 2010; Pilfold et al., 2014; Smith and Stirling, 1975; Wiig et al., 1999). Thus, for polar bears, the area of sea ice visited will better represent the resource aspect of their home ranges than the geographic area.

In this Chapter, I develop a method to estimate the area of sea ice visited by polar bears. I compare these estimates to the sizes of bears' geographic home ranges. First, I show that mean area of habitat encountered is significantly larger than that of the geographic home range, but that the area of ice encountered by individuals can range from less than 3/4 to twice the size of the geographic home range. Second, I show that although the areas of both the geographic home range and the habitat encountered are associated with some of the same environmental covariates, only the area of habitat encountered is correlated with the amount of ice drift. Finally, I show that by incorporating drift to create an estimate of habitat encountered I increase the amount of variation explained when relating the home range size to intrinsic and extrinsic covariates.

5.2 Methods

5.2.1 Polar bear GPS data

I used the movement data of 21 polar bears collared in the Beaufort Sea from April and May 2007-2011 to estimate annual home ranges. The bears were located by helicopter and immobilized using standard methods (Stirling et al., 1989). Collars (Telonics Inc., Mesa, AZ) were programmed to collect a GPS location every 4 hrs for one or two years. Following immobilisation, most bears recover their normal movement within three days of capture (Thiemann et al., 2013). Thus, I excluded locations during this period. Any subsequent capture event ended the data series for that bear. I limited the analysis to individuals that had data for close to a whole year, and only included bears if the collar functioned for ≥ 343 days. In addition, to insure that home range estimates were based on similar data sets, the analyzed bear were restricted to those with ≤ 8 consecutive days of missing data. As the calculation of the home range estimates depended on daily sea ice drift data at the location of the bear, I also excluded any bear year that were missing more than 150 days of drift data (see below for sea ice data description). I had sufficient data from five individuals to create multiple annual home ranges. For these, I selected the year that had the least missing sea ice data.

5.2.2 Sea ice movement data and differentiating drift from voluntary movement

One of my primary objectives was to incorporate ice drift into my home range analyses. I used polar pathfinder daily 25 *km* Ease-Grid sea ice motion vectors (Fowler, 2003). These 25 by 25 *km* pixel rasters provide estimates of the daily movement of sea ice in terms of displacement in the x and y direction. These estimates are based on varied sources of data, including Special Sensor Microwave/Imager and the International Arctic Buoy Programme buoy data (Fowler, 2003). I interpolated the ice drift value at each bear location with the *iwd* function of the R 3.0.2 (R Development Core Team, 2012) package *gstat* (Pebesma, 2004), setting the distance weighting power to 3. All locations with fewer than three pixels with drift data within 36 *km* were categorized as missing data. Pixels that lacked sea ice movement data did so because of proximity to water, the coast, or low ice concentration, which makes the estimation of sea ice movement by satellite imagery difficult (Schwegmann et al., 2011). Many missing data are close to the coast, in areas where stationary landfast ice is found in winter and spring. I identified instances where missing ice movement data were on landfast ice using Canadian Ice Service Arctic Regional Sea Ice Charts (Canadian Ice Service, 2009) and assigned a drift of 0 to these locations.

To incorporate drift in my home range analysis, it was important to differentiate the voluntary movement of the bear from movement caused by sea ice drift. The movement observed from the collar is a combination of both voluntary movement and drift (Gaspar et al., 2006). To estimate the voluntary movement, I subtracted the daily displacement of the sea ice from the observed daily collar displacement (Fig. 5.1B). Both missing collar locations and missing sea ice data precluded the estimation of the daily voluntary movement of a bear. Data gaps ≤ 8 days required interpolated locations for missing days and I used the straight-line distance between the two most recent locations. For days with missing sea ice data, I used the observed displacement of the collar as an estimate of the voluntary movement of the bear. This may result in underestimates of the difference between the geographic home range size and area of habitat encountered

5.2.3 Estimating the area of the geographic home range and of the habitat encountered

Both the area of the geographic home range and of the habitat encountered were estimated using a utilisation distribution with fixed bivariate normal kernel (Worton, 1989). For the smoothing parameter, h, I used the maximum observed daily displacement of each bear (range: 8.4 - 32.2 km/day). I used the observed collar displacement as it represents both the movement of the bear and the ice drift, which affects both the geographic area and the habitat encountered. I chose the maximum observed displacement because more commonly used methods did not converged or gave nonsensical results. The smoothing parameters estimated with the reference bandwidth method were much larger than the maximum observed displacement, resulting in over-smoothed home ranges. The least-square cross-validation method had convergence problems for many individuals and under-smoothed the home range of the others. The problems associated with these methods have been discussed elsewhere (see Hemson et al., 2005; Kie, 2013). I used the 95% contour of the utilisation distribution to delineate the home range. These calculations were made using the package *adehabitatHR* (Calenge, 2006).

The main difference between the two area estimates lies in the locations used to calculate the utilisation distributions. For the geographic home range, I used the observed and interpolated collar locations (Fig. 5.1A). For the habitat encountered, I used the locations associated with a movement path recreated from the voluntary movement of the bear (Fig. 5.1C). I wanted to determine if and how the area of sea ice habitat encountered by individual bears differed from their geographic home range. The two estimates were not normally distributed, so I compared them using a Wilcoxon Signed Rank test for paired samples ($H_0 : area_{\text{HE}} = area_{\text{GHR}}, H_a : area_{\text{HE}} > area_{\text{GHR}}$).

5.2.4 Identifying the determinants of home range size

I wanted to assess the determinants of home range size and whether these differed between the geographic home range and the area of ice habitat encountered. To do this, I used multiple linear regressions with a variety of intrinsic and extrinsic variables. The intrinsic variables I assessed were age class (adult, subadult), sex, and whether or not a cub accompanied the individual at the beginning of the time series. I included age class and sex as explanatory variables because similar factors have been investigated in the movement of individuals (Amstrup et al., 2000; Laidre et al., 2012; Mauritzen et al., 2001). The majority of the individuals collared were adult females, however some were subadults of either sex. I included the presence of cubs because caring for young can alter home range patterns (Mitchell and Powell, 2007; Tufto et al., 1996). In two instances, I selected the second year of movement data because it was of better quality than the first (see above) and thus I could not ascertain whether cubs accompanied the females at the beginning of the year. Following Mauritzen et al. (2003), I assigned cub status in these cases based on the normal reproductive cycle of polar bears and whether there was evidence for denning in the movement path. Polar bears only den to give birth to cubs and females from the Beaufort Sea normally weaned their young at 2.5 years of age (Stirling, 2002). As bears with cubs-of-the-year have different movement patterns and habitat preference than other females (Amstrup et al., 2000; Pilfold et al., 2013), cub age might be an important explanatory variable. However, my small sample size of cubs in certain age classes limited my analysis to presence/absence of cubs.

The extrinsic factors I assessed included both static and dynamic features of the habitat. The static features were the mean ocean depth within the geographic home range and whether the bears spent more than a week on land, the latter denoted by a binary variable. I estimated the mean ocean depth using the International Bathymetric Chart of the Arctic Ocean version 2.23 with 2 by 2 km grid cells (Jakobsson et al., 2008). My two dynamic covariates were associated with sea ice features: mean daily drift experienced by a bear (described above) and a proxy for the proportion of good sea ice habitat that an individual encountered. To assess the quality of the sea ice habitat, while also accounting for the daily changes in sea ice quality, I used the proportion of days that a bear spent at sea in ice concentration > 85%. I used this threshold to be consistent with Sahanatien and Derocher (2012) who used 85% ice concentration to define the best polar bear habitat. They also used a threshold of 60% ice concentration to designate good habitat. Because preliminary analyses indicated that this second threshold was highly correlated with the 85% ice concentration variable and performed less well, I excluded it from my final analysis. I used daily estimates of sea ice concentration for 25 by 25 km pixels generated from satellite brightness temperature data (Cavalieri et al., 1996). For the analysis of the area of sea ice encountered, I used an additional variable, the number of days with missing sea ice data, to account for its potential effect on my estimates.

Before conducting my analyses, I assessed collinearity between my predictor variables, using the correlation coefficient, r, as an indicator and the commonly used threshold of $|r| > 0.7$ (Dormann et al., 2013). None of the variables in my final analysis were collinear.

To identify which covariates are important determinants, I fit a series of linear regression models. I examined all combinations of covariates, because I had no a priori expectation for combinations of variables that would produce the best model. Moreover, I wanted to assess the relative importance of different variables using their importance weights, which requires that all variables be used in an equal number of models (Burnham and Anderson, 2002). Because of my small sample size, I did not include interactions between covariates. I compared the relative fit of the models using AIC_c (Burnham and Anderson, 2002). I evaluated the absolute fit using R^2 and by testing whether each variable in the best models was statistically significant.

All analyses and spatial data manipulations were performed in R 3.0.2 (R Development Core Team, 2012), and relied heavily on the *sp*, *raster*, and *rgdal* packages (Bivand et al., 2013; Hijmans, 2013; Pebesma and Bivand, 2005). All spatial analyses used the Northern Hemisphere azimuthal equal-area EASE-Grid map projection developed by the National Snow and Ice Data Center for polar sea ice data (Brodzik and Knowles, 2002).

5.3 Results

On average, the area of habitat encountered (232 597 km^2, range: 15 109 - 466 823 km^2) was significantly larger than that of the geographic home range (202 442 km^2, range: 14 983 - 472 287 km^2; Wilcoxon test, V=42, $p < 0.01$; Fig. 5.2A). However, the magnitude of the difference between these two area estimates ranged widely among individuals (126 - 102 000 km^2). Two thirds of the individuals (14/21) had larger areas of habitat encountered, while the rest had larger geographic home range areas (Fig. 5.1B). When travelling on ice, the annual average drift experienced by individual bears ranged between 2.3 and 8.0 km/day (mean = 4.5 km/day). The annual average of individuals' voluntary movement ranged from 4.1 to 21.5 km/day (mean = 13.9 km/day).

The variation in geographic home range area was largely explained by mean ocean depth and time spent on land. Depth and land were the only two covariates in the best model, were in most models with $\Delta AIC_c \leq 4$, and also had the highest importance weights (Tables 5.1 and 5.2). F-tests revealed that removal of either of these variables significantly reduced model fit (Table 5.2). Geographic home range size increased with mean depth, regardless of whether mean depth was investigated alone, or while accounting for the effect of the land covariate (Fig. 5.3A,C). Bears that spend more than a week on land had smaller home ranges than those that did not (Fig. 5.3B,D). Together, these two variables explained a large part of the variation in the size of geographic home ranges ($R^2 = 0.69$).

The variation in area of habitat encountered was largely explained by mean ocean depth, time spent on land, and mean daily ice drift. Depth, land, and drift were the only three covariates of the best model, were in all but one of the models with

$\Delta AIC_c \leq 4$, and had the highest importance weights (Tables 5.1 and 5.2). Removal of any of the variables significantly reduced the fit of the model (Table 5.2). As for the geographic home range area, the area of habitat encountered increased with depth, and if the bear spent ≤ 1 week on land (Fig. 5.4A,B,D,E). The area of habitat encountered also increased with increasing ice drift (Fig. 5.4C,F). These three variables explained a large part of the variation in the area of habitat encountered by different bears ($R^2 = 0.80$). I was better able to explain variation in the area of habitat encountered than geographic home range size even if I only used the variables in the best model for the geographic home range size ($area_{HE} = \beta_0 + \beta_1 depth + \beta_2 land$, $R^2 = 0.75$).

5.4 Discussion

The home range concept is characterised by two central aspects: 1) the importance of familiarity and fidelity in animal space use, and 2) a representation of the habitat space animals need to survive and reproduce, which can be used to assess the costs and benefits of using that space. For terrestrial animals, these two aspects of home ranges are spatially linked because the habitat within familiar geographic areas is motionless and relatively stable over time. Ecologists can thus delineate the space familiar to an animal at the same time as the amount of habitat required for survival and reproduction. For species such as the polar bear, which inhabit drifting habitats, the geographic link between these two aspects is lost. While space use analyses based on geographic locations can capture the fidelity of an individual to a certain region, they inadequately quantify the amount of habitat an individual encounters in moving habitats.

Because sea ice drifts in and out of a bear's geographic home range, the amount of ice habitat it encounters and the amount of energy it requires to reach resources will depend largely on whether it is moving with or against sea ice. The sea ice is the prime habitat polar bears use to forage (Derocher et al., 2004; Stirling et al., 1993; Stirling and Derocher, 2012). Thus, it is difficult to use home range size as an indicator of polar bear's habitat, resources, and energy expenditure without considering ice drift. I have presented a new means to estimate the area of habitat encountered for animals that inhabit drifting sea ice. My results for polar bears indicate that most individuals encountered more habitat than estimated by the geographic home range, and that in extreme cases the difference between these two estimates were close to 100 000 km^2 (i.e., > 50% of the mean geographic home range size). I was able to explain more of the individual variation in area of the habitat encountered than that of the geographic home range. This suggests that correcting home range area estimates with drift information is important in facilitating our understanding of the factors that govern polar bear space use.

5.4.1 Population and individual differences in area estimates

Polar bears have geographic home ranges orders of magnitude larger than expected for terrestrial carnivores of similar weight (Ferguson et al., 1999). This suggests that polar bears require more space than terrestrial carnivores to acquire resources. It also suggests that they can energetically afford to travel long distances to reach resources, even though the metabolic cost of walking is unusually high for polar bears (Hurst et al., 1982). Because previous home range size estimates did not correct for sea ice drift, the larger home ranges of polar bears could have resulted from bears passively drifting over large geographic areas. Thus, accounting for ice drift could have revealed that polar bears use a similar amount of habitat to terrestrial carnivores. My results suggest that this is not the case. My estimates of the area of habitat encountered were generally larger than my estimates of geographic home range size, although both estimates fell within the range estimated by others (e.g., Amstrup et al., 2000; Ferguson et al., 1999). This is consistent with results from Mauritzen et al. (2003) indicating that the observed displacement of polar bears is dominated by voluntary movement rather than passive drift. These findings support the suggestion that polar bears require a larger area of habitat than their terrestrial counterparts, and that factors such as large seasonal changes in habitat quality might force polar bears to travel long distances to maintain access to food resources (Ferguson et al., 1999).

The larger size of the area of habitat encountered compared to the geographic home range suggests that bears generally move in the opposite direction to the ice. Such movement behaviour has been shown in the Barents Sea, where there is a continuous southward ice drift, and this behaviour was suggested to be necessary for bears to remain in ice-covered habitat (Mauritzen et al., 2003). In the Beaufort Sea, it is less obvious that moving against the clockwise sea ice drift caused by the Beaufort gyre would be necessary for bears to avoid ice-free regions (Coachman and Aagaard, 1974). Polar bears, including those from the Beaufort Sea, exhibit site fidelity. They return to the same geographic region annually, use the same core area across years, and follow similar movement patterns between seasonally important regions (Amstrup et al., 2000; Born et al., 1997; Mauritzen et al., 2001; Stirling, 2002; Wiig, 1995). Thus, bears may walk against sea ice drift to remain within a familiar geographic region. However, this behaviour could also be explained by bears following cyclical changes in the spatial distribution of good habitat. Previous research in the Barents Sea has shown that the magnitude of bear displacement and ice drift were not correlated, suggesting that tracking of good quality habitat, rather than fidelity to a particular geographic region, was the primary driver of such behaviour (Mauritzen et al., 2003).

Regardless of what causes bears to move against the sea ice, my results indicate that most bears encounter more habitat than their geographic home range would suggest. These results highlight that the geographic home range is usually not an adequate representation of the ice habitat a bear covers in a year. The difference between the estimates of area of habitat encountered and geographic home range area spanned three orders of magnitude, with some individuals displaying the reverse pattern from the majority of the population (i.e., appear to encounter less habitat than estimated with geographic locations). The individual variation further emphasizes that studies of the physiological and ecological factors affecting home range size should account for the drift experienced by each bear.

5.4.2 Determinants of home range area

The home range sizes of polar bears are highly variable, ranging from a few hundred to several hundred thousand square kilometres (e.g., Ferguson et al., 1999; Mauritzen et al., 2001). Previous investigations of the determinants of home range size found that two factors were important in explaining this intraspecific variability. Home range size is influenced by both the amplitude of the seasonal change in ice extent, and whether an individual responds to the sea ice retreat by taking refuge on land (Ferguson et al., 1999; Mauritzen et al., 2001). These relationships reflect polar bears' use of sea ice as a platform to hunt seals and requirement for high sea ice concentration to travel effectively (Derocher et al., 2004). Although bears can swim long distances, swimming requires more energy than walking on ice and the drop in body temperature associated with being in the water is dangerous for cubs (Durner et al., 2011; Monnett and Gleason, 2006). When the sea ice melts in the summer, many bears avoid open water and low ice concentration by either moving onto land or migrating to areas of higher ice concentration (e.g., Cherry et al., 2013; Mauritzen et al., 2001).

An important part of the variation in polar bear home range size has been explained by large population differences in terms of the seasonal ice dynamics (Ferguson et al., 1999). For example, Arctic Archipelago bears experience less temporal variation in ice cover and have smaller home ranges than bears exposed to the large flux in ice extent of the Baffin Bay. The highly dynamic ice of the Beaufort Sea likely explains why my home range estimates, and those of Amstrup et al. (2000), are at the higher end of the size spectrum. Not all variation in home range size can be ascribed to population differences. Large intrapopulation variation in the Barents Sea has been attributed to individual specialization, with pelagic bears making long movements north to follow the retreating sea ice and nearshore bears taking refuge on land (Mauritzen et al., 2001). My results and those of Amstrup et al. (2000) show that bears in the southern Beaufort Sea have less variation in their home range size. In addition, all of my bears, except for three females likely to have denned, remained on the sea ice during low-ice periods. This suggests that broadly defined habitat specialization might not as easily differentiate the space use strategies of the bears in my population. I investigated the covariates that might explain the subtler differences in home range size of Beaufort Sea polar bears and found that mean ocean depth, time spent on land, and ice drift were important predictors of my area estimates.

Ocean depth was positively correlated with both the geographic home range area and area of habitat encountered, which may be explained by three mechanisms. First, it could be driven by spatiotemporal differences in seasonal ice melt. Bears experiencing larger seasonal flux in ice extent may have larger home ranges because they need to move further offshore, to deeper regions, to remain in ice-covered habitat. Most of my bears used overlapping regions of the Beaufort Sea, suggesting that they experience, and would have to react to, relatively small differences in seasonal ice extent. Second, the relationship could result from individual differences in strategies used to cope with seasonal ice loss. As mentioned above, bears in my sample did not use of land as a refuge during the low-ice season. However, some of them remained close to the coast, while others ranged far offshore. These differences might involve a trade-off. Bears staying in shallower regions travel less and have smaller home ranges, but they might be exposed to low sea ice concentration and the risk of being caught in open water. In that case, we would expect depth to act as a proxy for the time bears spend in good habitat. However, depth was not strongly correlated with the proportion of days in high ice concentration (Pearson correlation: 0.24), nor was the latter variable important in my analyses. Using yearly estimates for these variables may have masked relationships that occur during the low sea ice season and could be uncovered with analyses of seasonal home ranges. Third, the relationship may result from a decrease in foraging habitat quality with depth. The diet of polar bears in the Beaufort Sea comprises seal species that are most abundant in the relatively shallow waters of the continental shelf (Frost et al., 2004; Pilfold et al., 2012; Stirling et al., 1977; Thiemann et al., 2008). Theory predicts that individuals in poorer habitat should compensate for lower resource density with larger home ranges (Ford, 1983). My results are consistent with this hypothesis, but seal density is not linearly related to depth. A better test of this hypothesis, and a more complete analysis of home range determinants, would require extensive data on seal distributions. The relative importance of these three mechanisms is unclear. Nevertheless, there is a clear relationship between depth and polar bears' space use patterns. It is an important variable in predicting polar bear habitat use (Durner et al., 2009) and a strong predictor in my analyses of home range size.

The area of habitat encountered by bears and the size of their geographic home range also depended on whether a bear spent more than a week on land. Those that did had smaller home ranges. In previous studies, the influence of time on land on home range size was generally associated with bears taking refuge during the ice-free season (Ferguson et al., 1998, 1999; Mauritzen et al., 2001). This appears not to be the case in my study. Of the four bears that made extensive use of land, two of them denned and one had a movement pattern consistent with the use of a maternal den. The fourth female remained in the same location from December 10th to February 9th, less than the usual time spent in a den. This is suggestive of a failed reproductive event or the use of a winter shelter (Amstrup and Gardner, 1994; Messier et al., 1994). These results suggest that these females had small home ranges because they spent multiple months immobile on land and are consistent with previous findings that denning females have small home ranges (Mauritzen et al., 2001).

Although none of the intrinsic variables appeared to be important predictors, the smaller home ranges of denning females indicate that reproductive status affects polar bears' space use. Moreover, the only female from my sample that had cubs-of-the-year at capture was also the only bear that had a much larger geographic home range than area of habitat encountered (Fig. 5.2B). This suggests that her movement was dominated by drift. One potential explanation is that her cubs could not walk at a speed sufficient to counteract ice drift. Females with cubs-of-the-year move shorter distances and normally choose more stable landfast ice than other females (Amstrup et al., 2000; Pilfold et al., 2013; Stirling et al., 1993). This choice may prevent these females from drifting, and might have contributed to their underrepresentation in my data set due to missing ice data close to the coast.

The last covariate that appeared to be an important explanatory variable was ice drift, which had a significant positive relationship with area of habitat encountered, but was not important in explaining geographic home range size. These results suggest that polar bears compensate for ice drift. This behaviour has two implications. First, it suggests that bears exposed to higher levels of ice drift walk more to cover the same geographic area. If food resources are geographically fixed, such bears expend more energy to acquire the same amount of food. Second, compensating for ice drift means that with increased movement, there is an increased amount of ice habitat encountered. Polar bears heavily use drifting ice habitat, where they kill a significant proportion of seals (Pilfold et al., 2014; Stirling et al., 1993). Bears walking against faster moving ice will encounter more resources if seals are tied to the ice, as is the case of ringed seals when they maintain breathing holes and lairs (Kelly et al., 2010; Smith and Stirling, 1975), and the ice encountered has the same level of seal density. This increase in foraging opportunities may counteract the cost of walking against ice drift. Thus, the costs and benefits of compensating for ice drift will depend on whether seals are more tightly linked to particular geographic areas or particular ice floes, as well as how seals' space-use strategies are affected by differences in ice drift. Nevertheless, the impacts of drift on polar bear space use identified with my estimates of habitat encountered have implications on both their energy expenditure and food intake. The importance of drift on polar bear space is also emphasized by its large magnitude (4.5 km/day) relative to the bears' voluntary movement (13.9 km/day).

5.4.3 Challenges involved in incorporating drift in home range analyses

I presented a first attempt to incorporate drift into home range analyses. My estimate serves as better approximation of the ice habitat encountered, and of the movement required to access resources, than assuming the sea ice is immobile, as using the geographic home range does. However, this approach could be developed further. My estimate is based on the simplifying assumption that ice drifts as one large piece, or many pieces moving in unison, and thus that the voluntary movement of the bears maps the amount of ice encountered. This assumption may be met for large parts of the year when the Beaufort Sea is composed of westward moving floes wider than 2 km (Canadian Ice Service, 2009). However, sea ice fractures and compresses, wind affects the direction of ice drift, and sea ice configuration can change rapidly during break up (Comiso, 2010). Although logistically challenging, further developments could account for these factors by modeling the movement of individual floes. Any estimates will depend on the availability, accuracy, and spatiotemporal scale of ice drift data. Sea ice data is generally accurate, but can be inaccurate or unavailable close to the coast and where ice concentration is low (Schwegmann et al., 2011). In addition, the ice drift data I used is only available at coarse spatial scale, and on a daily basis. Improved ice drift data would enable us to refine estimates of the area of ice habitat encountered.

One of the reasons polar bears are thought to have large and variable home ranges is that they depend on the marine environment, which is highly variable in space and time (Ferguson et al., 1999). Perhaps because of the complexity associated with studying the space-use patterns of marine animals, comparatively fewer home range studies have been performed on marine than terrestrial species. Studying the home range of marine animals will require us to differentiate between the trade-offs of using resources that are geographically fixed and those that are drifting. My method is directly applicable to other species walking on the sea ice (e.g., arctic foxes, *Vulpes alopex*, Pamperin et al., 2008) and useful for other ice-dependent species, such as ringed seals. The more fluid and three-dimensional ocean will present additional challenges. However, the concepts presented here can serve as a foundation for new approaches to study the space-use of marine species.

Table 5.1: Relative fit of the best models ($\Delta AIC_c \leq 4$) explaining the area of the geographic home range and of the ice habitat encountered.

Covariates included	df	ΔAIC_c	Akaike weight
Geographic home range area			
depth + land	4	0.00	0.325
depth + good ice	4	1.52	0.152
depth	3	1.87	0.128
depth + land + sex	5	2.78	0.081
depth + land + cub	5	3.14	0.068
depth + land + drift	5	3.22	0.065
depth + land + good ice	5	3.29	0.063
depth + drift	4	3.35	0.061
depth + land + age	5	3.48	0.057
Area of habitat encountered			
depth + land + drift	5	0.00	0.459
depth + land	4	1.93	0.175
depth + land + drift + iceNA	6	3.12	0.096
depth + land + drift + cub	6	3.69	0.073
depth + land + drift + sex	6	3.82	0.068
depth + land + drift + age	6	3.92	0.065
depth + land + drift + good ice	6	3.94	0.064

Table 5.2: The model averaged coefficient and importance weight of all covariates investigated. The average coefficients and their confidence intervals (CIs) are based on the Akaike weight of all models investigated. The F-value and p-value associated with testing whether the variables in the best model significantly change the fit of the model. The variables in the best model of each area are bolded.

Covariate	Coefficient	CI	Importance weight	F-value	p-value
Geographic home range area					
age (subadult)	2.87	-7.33-13.08	0.18	–	–
cub (true)	-1.98	-9.37-5.41	0.17	–	–
depth	0.012	0.007-0.017	> 0.99	31.12	< 0.01
drift	1.04	-1.82-3.89	0.19	–	–
good ice	21.32	-15.52-58.15	0.31	–	–
land (true)	-7.93	-16.87-1.00	0.53	4.79	0.04
sex (male)	-3.88	-14.82-7.06	0.20	–	–
Area of habitat encountered					
age (subadult)	-0.053	-7.55-7.45	0.12	–	–
cub (true)	-1.71	-7.64-4.23	0.14	–	–
depth	0.009	0.005-0.014	> 0.99	20.10	< 0.01
drift	2.34	0.07-4.62	0.70	5.01	0.04
good ice	1.50	-40.26-43.25	0.13	–	–
ice NA	0.02	-0.06-0.11	0.15	–	–
land (true)	-12.47	-20.36--4.58	0.97	12.59	< 0.01
sex (male)	-0.71	-8.78-7.37	0.12	–	–

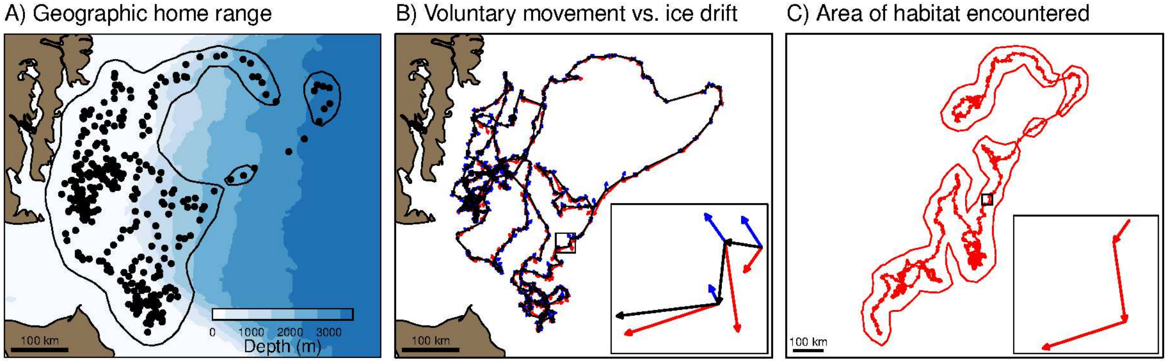

Figure 5.1: Representation of varied aspects of the home range of one polar bear. Panel A represents the geographic home range (—) and the locations given by the collar (•) on which it is based. The blue contour represents the bathymetry gradient of the region. Panel B represents the decomposition of the observed displacements of the bear (→) into their ice drift (→) and voluntary movement (→) components. Panel C represents an estimate of the area of habitat encountered (—) and the reconstructed voluntary movement path (→). Note that the projection of the map is Northern Hemisphere azimuthal equal-area EASE-Grid developed by the National Snow and Ice Data Center for polar sea ice data (Brodzik and Knowles, 2002).

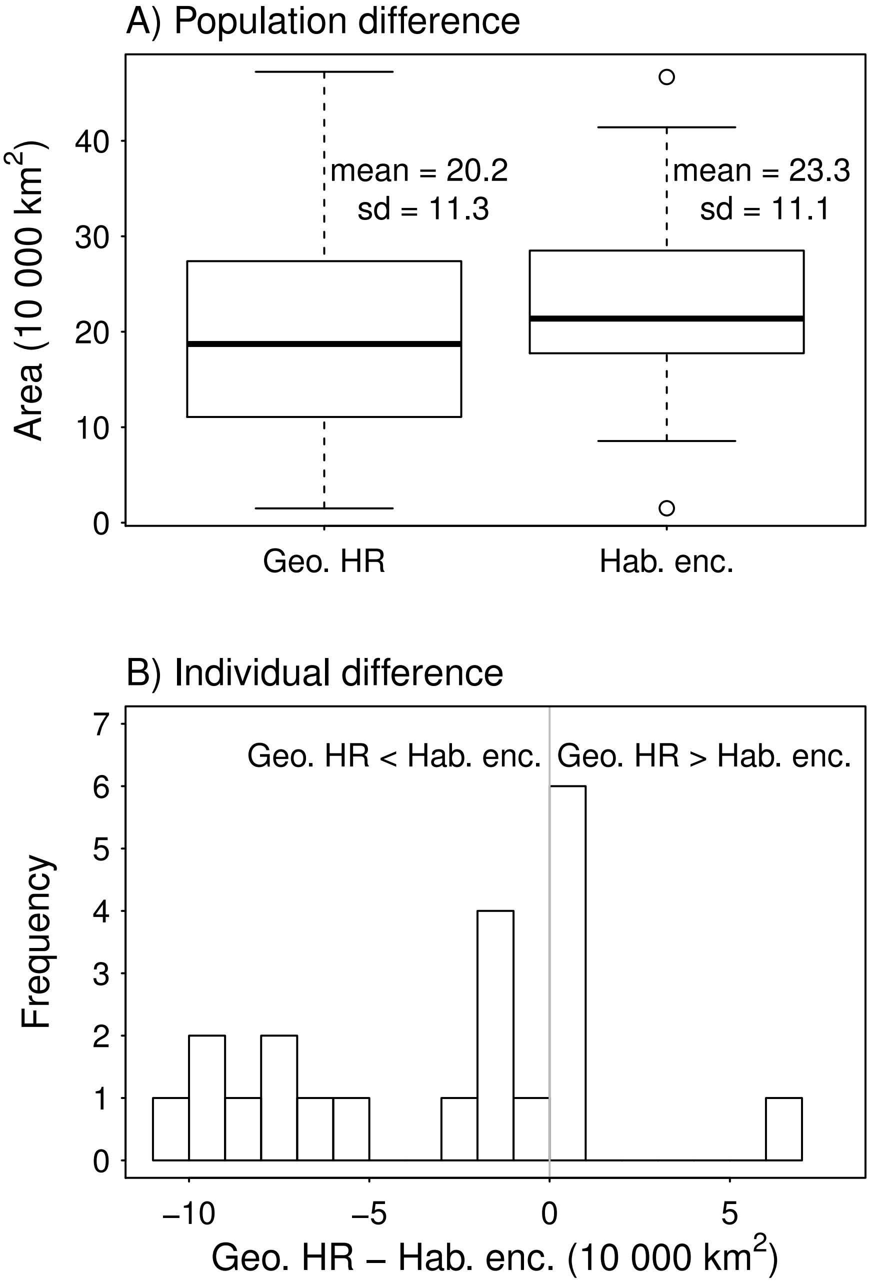

Figure 5.2: Differences between the size of the geographic home range and of the area of habitat encountered. Panel A represents the population difference between these two estimates. Panel B represents the differences between these two estimates for each individual, with positive differences indicating that the geographic home range is larger than the area of habitat encountered and negative differences indicating that the geographic home range is smaller than the area of habitat encountered.

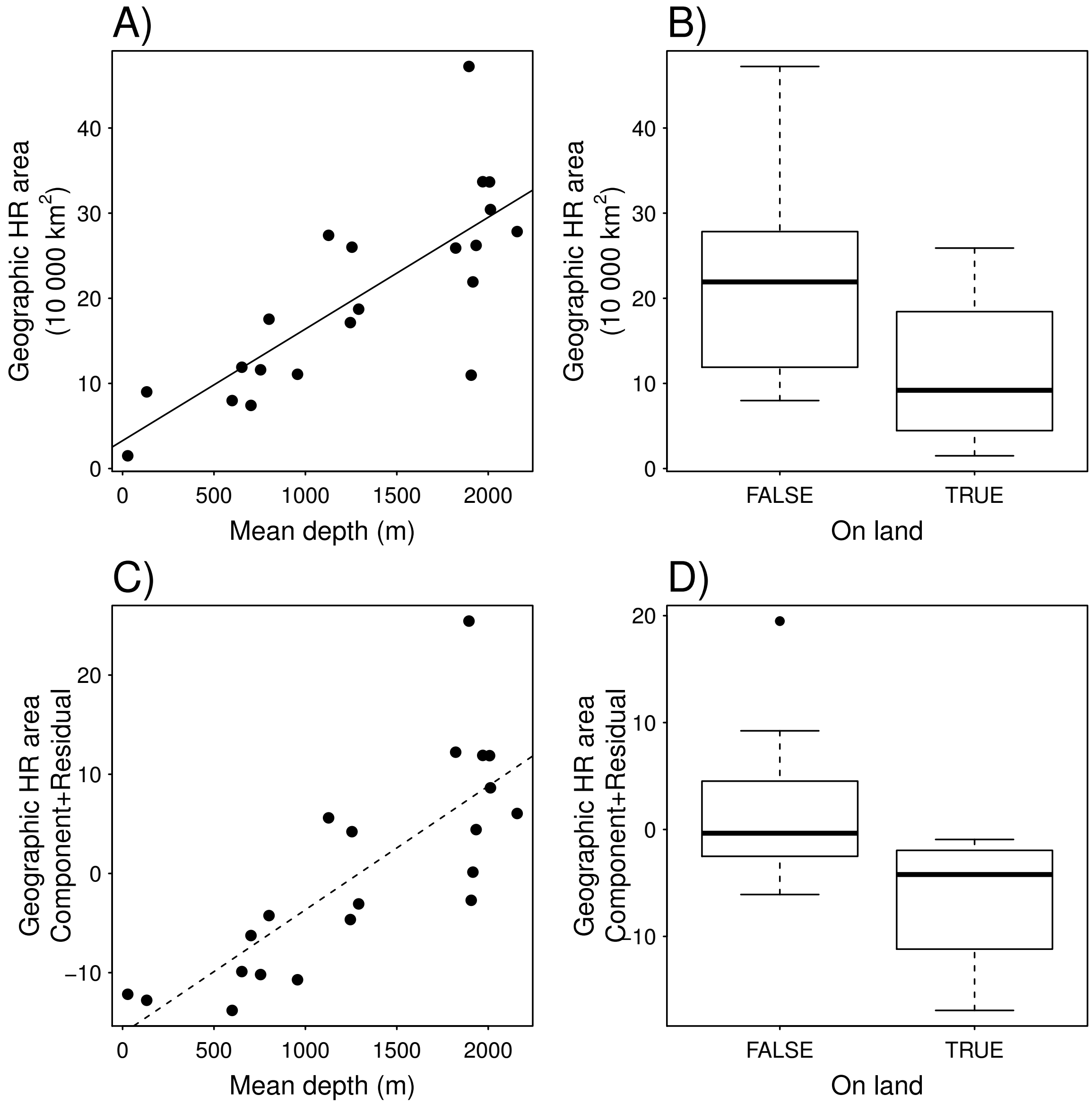

Figure 5.3: Relationships between the geographic home range and the covariates of its best model, mean depth (A & C) and whether the bear spend more than a week on land (B & D). Panels A & B represent the individual effect of each covariate, while panels C & D represent the effect when the other variable is accounted for.

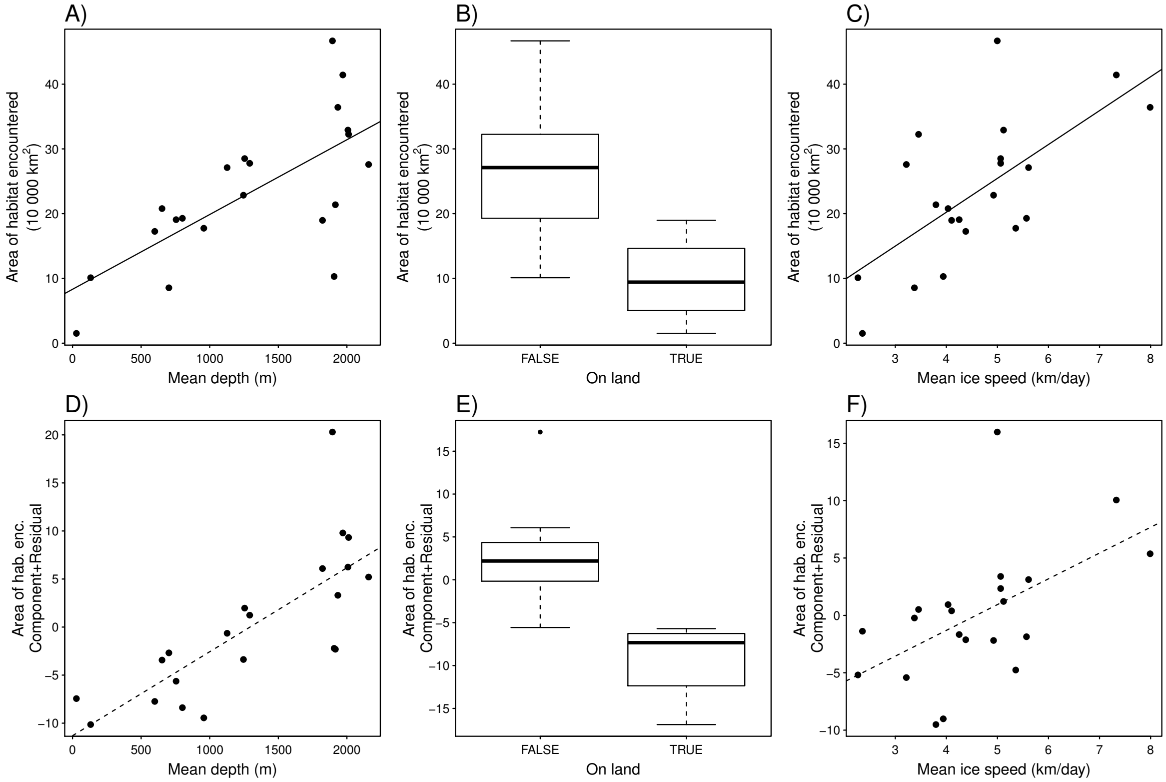

Figure 5.4: Relationships between the area of habitat encountered and the covariates of its best model, mean depth (A & D), whether the bear spend more than a week on land (B & E), and mean daily ice speed (C & F). Panels A, B, & C represent the individual effect of each covariate, while panels D, E, & F represent the effect when the other variables are accounted for.

Chapter 6

Using movement data to understand habitat use: currents frontiers and future prospects

Characterizing species' habitats is fundamental to our understanding of their distributions and to many other objectives of ecologists (Boyce and McDonald, 1999). Thus, ecology has long been a habitat-centered science (Noss et al., 1997). Habitat can be conceptualised as the area with the resources and environmental conditions necessary for individuals to survive and reproduce, and thus promote their occupancy (Hall et al., 1997; Morrison et al., 2006). Understanding species-habitat relationships is not only crucial to the field of ecology, it is essential for the management and conservation of species. The purpose of many environmental laws, such as Canada's Species at Risk Act and the United States' Endangered Species Act, is to provide a means to protect the habitat of endangered species (CSAR, 2013; ESA, 2003). Characterising a species' critical habitat is an important step in assessing whether human altered landscapes will maintain the features required for species to survive (Krausman, 1999). As such, the growing impacts of habitat fragmentation and climate change on ecosystems are increasing the significance of species-habitat studies in ecology and management (Betts et al., 2014; Guisan and Thuiller, 2005; Pearson and Dawson, 2003).

The enduring interest in species-habitat relationship has driven the development of a wide variety of tools to characterise a species' habitat (Elith and Leathwick, 2009; Guisan and Thuiller, 2005; Hirzel and Lay, 2008). For example, species distribution models, and their associated habitat suitability maps, range from simplistic models used to predict large-scale biodiversity patterns to detailed models used to identify important features of the local environment. For instance, impacts of climate change on continent-wide biodiversity can be predicted with bioclimatic envelopes, which focus primarily on the climate components of the fundamental niche of species (Pearson and Dawson, 2003). In contrast, identifying highway crossing zones for species of conservation priority requires the thorough habitat characterisation provided by tools such as resource selection functions and least-cost path analyses (e.g., Chetkiewicz and Boyce, 2009).

The appropriateness of different approaches depends on a species' mobility (Elith and Leathwick, 2009; Guisan and Thuiller, 2005). Characterising the environment of sessile organisms, or animals with small home ranges, is relatively simple compared to doing so for wide-ranging animals that can use patchily distributed resources (Elith and Leathwick, 2009). First, unlike sessile organisms that use a single habitat, vagile animals might require a set of different habitats to accomplish their diverse activities. For example, the nesting habitat of seabirds is distinct from the one they use to forage (e.g., Elliott et al., 2009; Weimerskirch et al., 1993). As such, evaluating the importance of a given habitat requires understanding how a species uses it. While species distribution models, such as resources selection functions, are useful for identifying the habitat where organisms can be found, they do not address why the animals use these habitats (Boyce and McDonald, 1999). Second, while it is trivial to quantify the amount of habitat required by a sessile organism, measures such as home range size are required for highly mobile animals. Considering an animal's home range size is important when constructing habitat suitability models, because small patches of suitable habitat might be insufficient for many large and wide-ranging species to survive (Gurnell et al., 2002; Hirzel and Lay, 2008). Movement and home range models, such as those described in my thesis, are increasingly used to relate habitat to specific behaviours and to quantify the amount of habitat that mobile animals require.

6.1 Understanding search strategies to better relate habitat to foraging behaviour

Models that categorise segments of movement paths into behavioural modes are used to relate habitat to specific behaviours (e.g., Breed et al., 2009; Frair et al., 2005; Morales et al., 2004). In particular, these movement models have been used to differentiate between foraging and travelling habitats. These models are often based on search strategy theory and the rarely tested assumption that foraging is associated with slow and tortuous movement, but not with fast and directed movement (Wakefield et al., 2009). However, a few studies showed that this assumption can be violated: some animals can successfully catch prey during fast and directed movement, and areas associated with putative foraging movement are not always related to prey capture or other foraging proxies (Catry et al., 2004a,b; Robinson et al., 2007; Thums et al., 2011; Weimerskirch et al., 2007). These results indicate that these models are at times inadequate for identifying foraging areas out of movement data, and that the search strategy they rely upon may be inappropriate for some species.

While most movement models used to identify foraging events are based on a single search strategy model, the area-restricted search (ARS, Dragon et al., 2012), many others have been suggested (e.g., Bell, 1991; Fronhofer et al., 2013; Nevitt et al., 2008; Zollner and Lima, 1999). The Lévy walk is a controversial alternative that has garnered significant interest in recent years, partly due to empirical evidence for this strategy in a large number of species (Focardi et al., 2009; Humphries et al., 2010, 2012, but see James et al. 2011). Unlike the ARS, the Lévy walk strategy does not predict that a forager will increase its tortuousity and decrease its speed after encountering a prey item. While the ARS and the Lévy walk make different assumptions on the relationship between movement and successful foraging events, they have similar emergent movement patterns and are difficult to differentiate (Benhamou, 2007; Plank and Codling, 2009). Thus, the use of the Lévy strategy by some species could partly explain why movement models based on the ARS cannot always predict foraging events (e.g., wandering albatross, *Diomedea exulans*, Humphries et al., 2012; Weimerskirch et al., 2007).

Research on the ARS and Lévy strategies has developed in parallel, with each strategy used by ecologists with different goals and modeled in different statistical frameworks. Recent work on the ARS has focussed on using its predictions to distinguish behavioural movement modes, with many methods using either metrics, such as first passage time, or Bayesian statistics (e.g., Dragon et al., 2012; Fauchald and Tveraa, 2003; Morales et al., 2004). In contrast, most recent Lévy walk studies have been directed towards finding empirical evidence for the search strategy itself, and often use information-theoretic tools such as maximum likelihood estimate and Akaike Information Criterion (AIC, e.g., Humphries et al., 2012; Sims et al., 2012). Finding empirical evidence for the Lévy strategy has been surrounded by controversy because many of the methods used in the past were flawed (Edwards, 2011; Edwards et al., 2012, 2007). Even recently proposed methods can misidentify movement produced by ARS as a Lévy walk (Auger-Méthé et al., 2014; Plank and Codling, 2009).

In Chapter 2, I argued that to differentiate between these two search strategies, we need to model them in a comparable statistical framework. In particular, I called for the development of a likelihood function for the ARS that can be directly compared to the Lévy walk model using tools such as AIC. Because the best model according to AIC may still be a poor model, I further argued that it is important to investigate the absolute fit of the best model. This is particularly important when movement models are used to identify a behavioural process, such as the underlying search strategy, rather than simply describing the movement pattern. This work has helped spur the development of new methods to differentiate the Lévy walk from the ARS (Plank et al., 2013; Reynolds, 2012) and to investigate the absolute fit of movement models (Potts et al., 2014). In addition, it has been used to emphasize the importance of investigating absolute fit in research overturning evidence for the Lévy walk (Edwards et al., 2012).

In Chapter 3, I developed a method to differentiate between the ARS and Lévy strategies. Although a number of useful methods have been developed concurrently, mine has a number of advantages. Some newly proposed methods focus on limiting misidentification errors when assessing evidence for the Lévy walk (Gautestad, 2012, 2013; Reynolds, 2012, but see Auger-Méthé et al. 2014). My method simultaneously assesses the evidence for both the Lévy walk and ARS. This reduces the potential for misidentification errors and provides a fuller investigation of animal search behaviour. Other new methods compare the Lévy walk to models similar to the ARS (Jansen et al., 2012; Plank et al., 2013). However, unlike my method, they do not model turn angles and behavioural autocorrelation. These two features are essential to accurately describe the ARS. My hope is that our ability to differentiate between these two prominent search strategies will further the understanding of how animal find resources. In addition, it could help assess the appropriateness of models used to identify foraging areas with movement data. While this method cannot replace testing whether putative foraging movement is associated with prey capture, it can be used to determine whether models based on ARS are likely to be appropriate for the animals studied.

To demonstrate the usefulness of the method, and gain insight into the search strategies used by different mammals, I applied it to the movement data of three species (Chapter 4). Although previous methods would have found evidence for the Lévy walk for some individuals, a comparison of the Lévy walk to the ARS showed stronger support for the latter. While the ARS was the best model of the vast majority of individuals, there was a range of support its absolute fit. The ARS was sufficient to explain the movement of nearly half of herbivorous caribou (*Rangifer tarandus caribou*) and a quarter of omnivorous grizzly bears (*Ursus arctos*), but was insufficient to explain the movement of all polar bears (*U. maritimus*), which are strict carnivores. Although this variation could be explained by multiple factors, including differences in sampling scales, it suggests that research into how feeding guilds differ in their search strategies may be fruitful.

The efficiency of many search strategies depends on the distribution of resources and whether a resource item is destroyed at capture (e.g., Bartumeus et al., 2002, 2005; Zollner and Lima, 1999). Characteristics of resources, such as their size, mobility, and gregariousness, can impact the time and energy animals allocate to searching, pursuing and handling prey (Bell, 1991). They are also likely to impact the efficiency of different search strategies. For example, slowing down and turning more often after encountering a berry bush might help an animal find other nearby bushes. However, this ARS movement is unlikely to provide further hunting opportunities after making a kill within a herd of ungulates, as the herd is likely to run away following the capture of one of its members. Some of these characteristics may be related to resources distribution and renewal, but their influence on the search strategies of different feeding guilds has not received much attention.

The empirical support for the ARS for the three species also suggests that separating habitat use analyses by behaviour could reveal relationships that would be obscured by analyses of the undivided datasets. Using models similar to ARS, Johnson et al. (2002*a*,*b*) found that the cover types, energetic costs, and predation risks differed between areas caribou used for “intrapatch” and “interpatch” movement. The cover types for the intrapatch movement were consistent with those where caribou are expected to forage. These findings combined with my results, suggests that some caribou might use ARS as a search strategy, and that this may be a species we should use to investigate whether actual foraging events are linked to putative foraging areas. Despite the ARS not being sufficient to explain the movement data of many individuals, it outperformed the three single-behaviour models for the three study species. This suggests that separating habitat analyses by behaviour could also be informative for grizzly bears and polar bears. Such analyses could help us understand how these animals are using different habitats and provide insights into why my ARS model was not adequate for some individuals.

Animals use perceptual cues and memory to navigate in their environment (e.g., Conover, 2007; Mendl et al., 1997). Long ranging perceptual abilities and knowledge of the environment are likely to make search strategies other than the Lévy and ARS optimal. Use of alternative strategies could explain why the ARS was insufficient to explain the movement of many individuals. Many alternative search strategies have been proposed in the literature, including systematic-, olfaction-, and memory-based strategies (Bell, 1991; Fronhofer et al., 2013; Nevitt et al., 2008; Zollner and Lima, 1999). Many of these may produce movement similar to both the Lévy and the ARS. Thus, a next step for future research would be to model these alternatives in the same framework used to differentiate the Lévy and ARS, so the empirical evidence for a broader selection of strategies can be directly compared. This could be particularly useful for species such as the wandering albatross, which has been suggested to use the Lévy strategy, olfactory search and, at small scales, ARS (Humphries et al., 2012; Nevitt et al., 2008; Weimerskirch et al., 2007). As additional search strategy models are developed, it may prove beneficial to consider how they could be used to identify foraging habitat. For this to be possible, the strategies must predict a change in movement behaviour when an animal is in proximity to food, as the ARS does. Current Lévy strategy models do not make such predictions, making them unsuited to this task. However, other strategies will involve predictable changes in relation to prey detection. For example, olfactory search models predict changes in movement relative to wind direction that could be used for such purposes (Nevitt et al., 2008). Such new movement models may provide more robust methods to detect foraging areas and habitat.

6.2 Measuring home ranges in moving habitats to quantify the amount of habitat animals require

Home range analysis aims to encapsulate the space animals use to reproduce and survive. Home range size is related to energetic requirements, as demonstrated by its allometric relationship with body size (Harestad and Bunnell, 1979; McNab, 1963). As a consequence, home range size is expected to depend on the density and distribution of resources, as well as on the cost of movement associated with reaching them (Ford 1983, Mitchell and Powell 2004). Thus, home range size is a key metric that can be use to measure how animals respond to environmental and habitat variation (e.g., Rivrud et al., 2010; Tufto et al., 1996; van Beest et al., 2011). Because of its importance in ecological and applied research, a variety of tools have been developed to study home ranges. These include tools for delineating home ranges, as well as methods relating home range size to habitat variables and traits of individuals (e.g., Börger et al., 2006; Getz et al., 2007; Worton, 1989). Understanding the factors affecting the home range size of animals living in moving habitats (e.g., ocean, atmosphere, rivers) is more difficult. As currents constantly move resources through an area, they can have a large influence on the amount of resources available, the energy expended in movement, and thus an animal's space use pattern. For example, animals are able to forgo movement where currents provide a steady stream of resources, making sessility a common trait among marine invertebrates. In contrast, currents do not renew the resources available to animals drifting with them. Moving against the flow can be energetically demanding, and the distance moved is not necessarily representative of the cost of locomotion (Gaspar et al., 2006). Thus, in moving habitats, variation in geographic home range size is less likely to represent differences in energetic requirements, locomotion costs, and animal behaviours.

In Chapter 5, I provided a first approximation of the effects of drift on home ranges using polar bears as my study species. Their interaction with the two-dimensional sea ice platform allowed for the simplifying assumption that the voluntary movement of bears maps the amount of ice encountered. Estimates of the area of habitat encountered confirmed that polar bears require more habitat than terrestrial carnivores, and showed that the geographic home range underestimates both the movement of bears and the amount of ice habitat that they encounter. The large individual variation in the difference between the estimates suggests that investigating only the geographic area used by bears and ignoring the area of ice habitat could lessen our understanding of the home range behaviour of polar bears. In particular, ice drift was an important covariate only when area of habitat encountered was investigated, and indicated that bears living in highly mobile habitat might be exposed to higher energetic costs, and potentially larger energetic gains, than bears inhabiting more stable ice.

Climate change is altering wind patterns and the magnitude of extreme conditions, leading to increases in the speed of ice drift in the Arctic (Spreen et al., 2011; Young et al., 2011). While we have a growing understanding of the negative impacts of sea ice loss on the survival and reproduction of polar bears (Stirling and Derocher, 2012), it is unclear how increasing ice drift might alter polar bears' resilience to climate change. For wandering albatrosses, faster wind speeds have led to increased movement rates, shifted distributions, and altered foraging and breeding success (Weimerskirch et al., 2012). As such, accounting for effects of climate change on drift may be critical for the management of species living in moving habitats.

Incorporating drift into the home range analyses of species other than polar bears is likely to be more challenging. For example, a full representation of marine space use involves three dimensions, and metrics such as two-dimensional home range size are likely to misrepresent the density of resources and the distances travelled by animals.

Moreover, while the assumption that ice moving as a solid and somewhat cohesive block is acceptable, such assumption is less reasonable in the more fluid habitats of rivers, oceans, and the atmosphere. Turbulence, mixing, and diffusion, change the composition and distribution of resources within water and air masses, and these small-scale processes are often obscured by the coarse spatiotemporal scale of the data available for these systems (Alvarez et al., 2013; Fossette et al., 2012). These factors will hinder using currently available information to map the amount of habitat space encountered by animals. Regardless of whether my method or other methods are most suited to address them, these habitats expose limitations to our understanding of animal space use. One of these is the importance of variability of resources in driving space use patterns. Ferguson et al. (1999) suggested that marine animals had large home ranges due to the variability of marine environments. Although habitat composition changes through time in terrestrial systems (e.g., snow cover, plant growth), it is often assumed that moving habitats, such as oceanic waters, have particularly high variability and low predictability (Weimerskirch, 2007). Small scale variability in habitat composition was typically ignored until researchers studying polar bears demonstrated that accounting for temporal changes in habitat availability improved resource selection analyses (Arthur et al., 1996; Moorcroft, 2012). Mueller and Fagan (2008) proposed a theoretical framework predicting population-level space use patterns based on large-scale resources dynamics. However, the impacts of small-scale variability in habitat composition on broad space use patterns, and whether it contributes to the larger home ranges of marine animals, remain to be investigated.

6.3 Accelerating progress by relating space-use patterns to field observations and fitness proxies

Movement and space-use models have enriched our understanding of how animals interact with their environment. In recent years, increasingly mechanistic models have allowed ecologists to relate complex animal behaviours with habitat and space-use patterns (e.g., Moorcroft and Lewis, 2006). Ecologists increasingly rely on satellite telemetry and mathematical models to understand species-habitat relationships, and the number of movement studies has boomed (Holyoak et al., 2008). As a consequence of the fast progress of this field, many methodological problems and new avenues have been overlooked. The research presented in this thesis identifies pitfalls in currently available methods and suggests improved approaches to understand search strategies and home range patterns. By applying these refined approaches to empirical data, this work demonstrates that species and individual differ in their search strategies and that drift influences the home range patterns of polar bears. My work also highlights a need for the development of new search strategy models, as well as space-use analyses that incorporate drift for a broader range of animals. Although there is ample space for further developments of both smaller scale movement models and larger scale space-use analyses, I believe that progress will accelerate with increased emphasis on combining these approaches with field observations and fitness data. This echoes a recent call for ecologists to link movement to population processes and ground-based observations of behaviour and resources (Hebblewhite and Haydon, 2010). Field observations allow us to evaluate our model assumptions and develop new hypotheses for space-use behaviours that may not be obvious from movement alone. Fitness proxies, such as brood size and changes in body condition, will allow us to link movement behaviour to their ecological and evolutionary consequences.

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Appendix A

Extended model set

As mentioned in Chapter 3 there exist non-truncated versions of the TLW, TBW, and TCRW. Unlike the truncated versions, the probability density function (PDF) of the non-truncated versions do not have an upper bound on step length size (Table A.1). Such difference is important for the Lévy strategy because the non-truncated Lévy walk (LW) has a non-negligible probability of extremely long step lengths. As mentioned in Chapter 3, only the TLW is biologically plausible (Viswanathan et al., 2008). However, the LW is often used as a model for the Lévy strategy in both empirical and theoretical studies (e.g., Bartumeus et al., 2005; Edwards et al., 2007). As the probability of infinitely long step lengths is negligible for the non-truncated Brownian walk (BW) and correlated random walk (CRW), such distinction is less important. However, to differentiate between the Lévy strategy and the null models based on the main characteristics of each model rather than on the potential presence of a sharp upper bound in the step length distribution, it is advisable to be consistent in the incorporation of a truncation point. While I focused on the truncated models in Chapter 3, in this Appendix I present analyses that also include their non-truncated versions. The only difference with the method proposed in Chapter 3 (section 3.2.1) is that I am fitting to data three additional likelihoods: LW, BW, and CRW (Table A.2). Unlike the TLW, the LW uses the non-truncated Pareto distribution, $\psi(l|\mu, a)$ (Table A.1). Similarly, unlike the TBW and TCRW, the BW and CRW use the non-truncated version of the exponential distribution, $\phi(l|\lambda, a)$ (Table A.1).

There is little difference between the results of the four-models method of Chapter 3 and seven-models method of this Appendix. When applied to the simulations of the CCRW and TLW, my method performed as well when the seven likelihoods were used. The Akaike weights could differentiate between the Lévy and ARS strategies.

The main difference was that the Akaike weights could not differentiate between the TLW and LW (Fig. A.1B) and thus the weights of these two models needed to be summed, $w_{\mathrm{LW}} + w_{\mathrm{TLW}}$, to represent the Lévy strategy. When I used the summed of the Akaike weights I had similar results to those presented in Chapter 3. When the CCRW was simulated, 90.1% of the Akaike weight values of the CCRW exceeded 0.99 and the summed Akaike weight value of the LW and TLW never exceeded 0.01 (Fig. A.1A). When the TLW was simulated, 96.8% of the summed Akaike weight value of the LW and TLW exceeded 0.99 (Fig. A.1B). While 3.2% of the Akaike weight value of the CCRW exceeded 0.01, only 0.2% exceeded 0.5. Again the frequency of these misidentifications increased with increasing μ_{T} values.

Similarly, there was little difference in the empirical results of both methods (compare Tables 3.3 and A.3). The Akaike weights of Bear 2 continued to show strong support for the CCRW over the other alternatives. The Akaike weights of Bear 1 continued to show that, although the CCRW was the best model, the TCRW, and its non-truncated version, were important alternatives. However, in this case, the summed Akaike weights of the CRW and TCRW showed stronger support than the CCRW and the CRW was had a $\Delta AIC_c < 1$ (Table A.3).

Adding new models does not affect the parameter estimates of the four models already presented in Chapter 3. However, two new parameters were estimated, λ and μ. These can be compared to the values of their truncated analogue, λ_{T} and μ_{T} (Table A.4). There was no important changes in the λ values, but the non-truncated μ values were bigger than their truncated version, μ_{T}.

In summary, including the likelihoods of the LW, BW, and CRW in my analyses did not change the overall results. My method could still differentiate between the Lévy and the ARS strategies. However, the method cannot reliably differentiate between the truncated and non-truncated versions of the same model.

Table A.1: Formulas for the PDFs used in the models and the restrictions on their variables and parameters. Tables 3.2 and A.4 describe the parameters.

Symbol	PDF	Restrictions
$\phi(l \mid \lambda, a)$	$\lambda\, e^{-\lambda(l-a)}$	$a \leq l, \quad \lambda > 0$
$\phi_{\mathrm{T}}(l \mid \lambda_{\mathrm{T}}, a, b)$	$\frac{\lambda_{\mathrm{T}}\, e^{-\lambda_{\mathrm{T}} l}}{e^{-\lambda_{\mathrm{T}} a} - e^{-\lambda_{\mathrm{T}} b}}$	$a \leq l \leq b, \quad \lambda > 0$
$\psi(l \mid \mu, a)$	$\frac{(\mu-1)\, l^{-\mu}}{a^{1-\mu}}$	$a \leq l, \quad 1 < \mu \leq 3$
$\psi_{\mathrm{T}}(l \mid \mu_{\mathrm{T}}, a, b)$	$\frac{(\mu_{\mathrm{T}}-1)\, l^{-\mu_{\mathrm{T}}}}{a^{1-\mu_{\mathrm{T}}} - b^{1-\mu_{\mathrm{T}}}}$	$a \leq l \leq b, \quad 1 < \mu \leq 3$ [†]
$v(\theta \mid \kappa)$	$\frac{1}{\int_{-\pi}^{\pi} e^{\kappa \cos(\theta)}\, d\theta} e^{\kappa \cos(\theta)}$	[‡] $\kappa > 0$
$v_0(\theta)$	$\frac{1}{2\pi}$	

[†] Although the truncated Pareto distribution allow for a greater range of values for μ_{T}, I am restricting its values to those relevant to the Lévy strategy.

[‡] 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.

Table A.2: Likelihood functions and number of parameters to estimates, k, of the seven models. These models include the four models of Chapter 3 and the three additional models used in this Appendix. Unlike Table 3.1 of Chapter 3 there are two different models describing the Lévy strategy, TLW and LW, as well as four null models, TBW, BW, TCRW, CRW. Table A.1 describes the PDFs, $\phi()$, $\phi_{\mathrm{T}}()$, $v()$, $v_0()$, $\psi()$, and $\psi_{\mathrm{T}}()$. Tables 3.2 and A.4 describe the parameters.

Model	Likelihood function	k
CCRW	$\begin{pmatrix} \delta_{\mathrm{I}} & 1-\delta_{\mathrm{I}} \end{pmatrix} \begin{pmatrix} \phi(l_1 \mid \lambda_{\mathrm{I}}, a)\, v_0(\theta_1) & 0 \\ 0 & \phi(l_1 \mid \lambda_{\mathrm{E}}, a)\, v(\theta_1 \mid \kappa_{\mathrm{E}}) \end{pmatrix} \prod_{t=2}^{n} \begin{pmatrix} \gamma_{\mathrm{II}} & 1-\gamma_{\mathrm{II}} \\ 1-\gamma_{\mathrm{EE}} & \gamma_{\mathrm{EE}} \end{pmatrix} \begin{pmatrix} \phi(l_t \mid \lambda_{\mathrm{I}}, a)\, v_0(\theta_t) & 0 \\ 0 & \phi(l_t \mid \lambda_{\mathrm{E}}, a)\, v(\theta_t \mid \kappa_{\mathrm{E}}) \end{pmatrix} \begin{pmatrix} 1 \\ 1 \end{pmatrix}$	7
LW	$\prod_{t=1}^{n} \psi(l_t \mid \mu, a)\, v_0(\theta_t)$	2
TLW	$\prod_{t=1}^{n} \psi_{\mathrm{T}}(l_t \mid \mu_{\mathrm{T}}, a, b)\, v_0(\theta_t)$	3
BW	$\prod_{t=1}^{n} \phi(l_t \mid \lambda, a)\, v_0(\theta_t)$	2
TBW	$\prod_{t=1}^{n} \phi_{\mathrm{T}}(l_t \mid \lambda_{\mathrm{T}}, a, b)\, v_0(\theta_t)$	3
CRW	$\prod_{t=1}^{n} \phi(l_t \mid \lambda, a)\, v(\theta_t \mid \kappa)$	3
TCRW	$\prod_{t=1}^{n} \phi_{\mathrm{T}}(l_t \mid \lambda_{\mathrm{T}}, a, b)\, v(\theta_t \mid \kappa)$	4

Table A.3: Relative fit of the seven models on the movement paths of two polar bears. For each bear, the ΔAIC_c and Akaike weight for each model and the summed Akaike weight for the models with both truncated and non-truncated versions.

Model	ΔAIC_c		Akaike weight		Summed Akaike weight	
	Bear 1	Bear 2	Bear 1	Bear 2	Bear 1	Bear 2
CCRW	0	0	0.47	1.00	0.47	1.00
LW	466.8	2465.0	< 0.01	< 0.01	< 0.01	< 0.01
TLW	302.4	1479.7	< 0.01	< 0.01		
BW	170.3	648.6	< 0.01	< 0.01	< 0.01	< 0.01
TBW	172.4	650.6	< 0.01	< 0.01		
CRW	0.4	137.2	0.39	< 0.01	0.53	< 0.01
TCRW	2.5	139.2	0.14	< 0.01		

Table A.4: Description and empirical estimates of the model parameters. Only the new parameters, λ and μ, and their truncated analogues, λ_{T} and μ_{T} are presented. See Table 3.2 of Chapter 3 for the other parameter estimates.

Symbol (unit)	Description	Bear 1	Bear 2
λ (m^{-1})	Rate parameter of the exponential distribution of the BW and CRW	0.0009 (0.0008-0.0010)	0.0010 (0.0009-0.0010)
λ_{T} (m^{-1})	Rate parameter of the exponential distribution of the TBW and TCRW	0.0009 (0.0008-0.0010)	0.0010 (0.0009-0.0010)
μ	Scale parameter of the non-truncated Pareto distribution of the LW	1.30 (1.26-1.34)	1.18 (1.17-1.19)
μ_{T}	Scale parameter of the truncated Pareto distribution of the TLW	1.00 † (0.93-1.07)	1.00 † (0.97-1.03)

† Because I used the quadratic approximation to estimate CIs, some CIs exceed the boundary of parameter space.

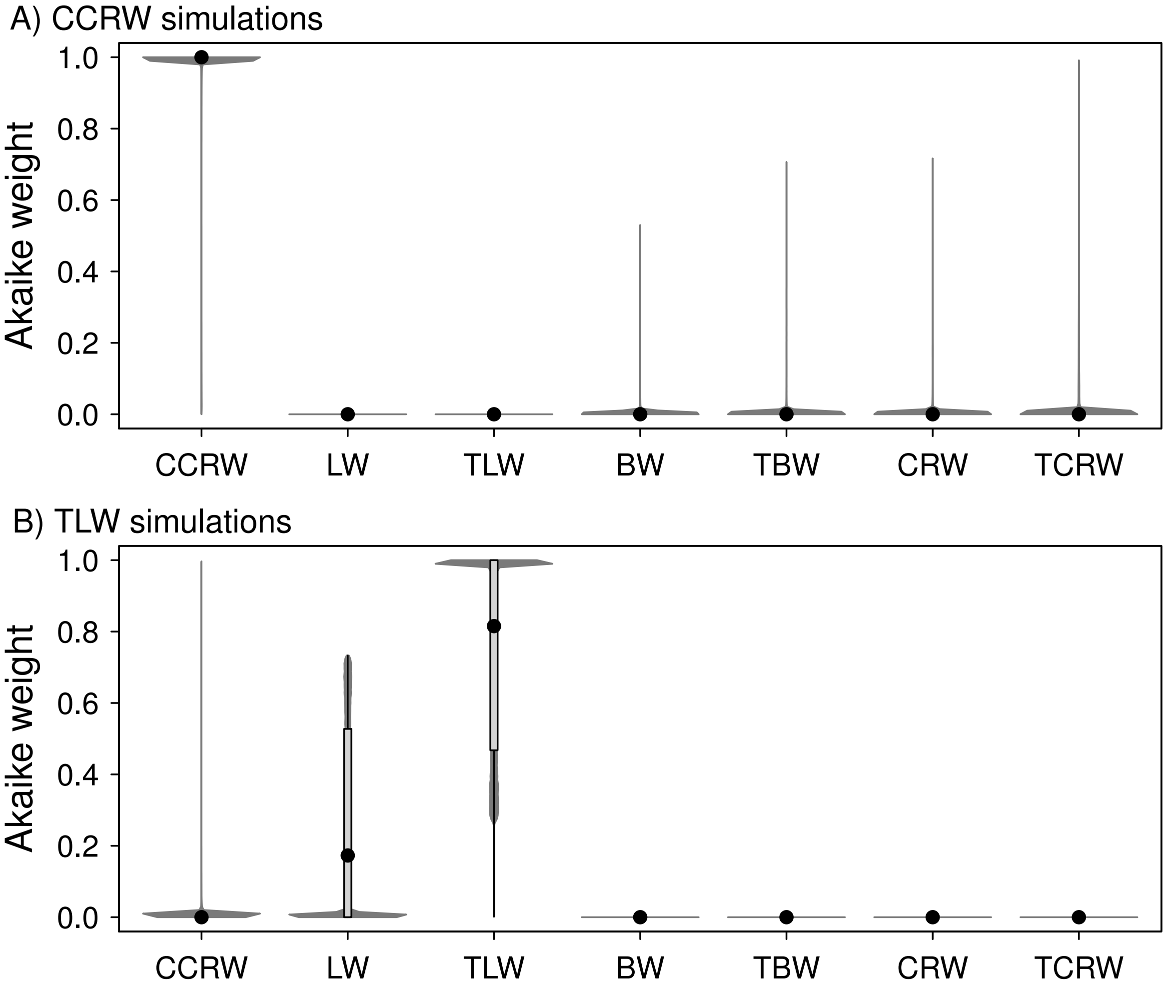

Figure A.1: Violin plots of the Akaike weights of each model for all simulated CCRWs and TLWs. High Akaike weight values represent strong support for a model relative to the other models. Violin plots are combinations of kernel density plots and box plots. Kernel density plots are represented by the dark gray polygon. Box plots are represented in black and light gray, with • identifying the median. Because the range of values for some models was orders of magnitude smaller than the y-axis, some box plots are only represented by their median. Panel A shows that for simulated CCRWs only the CCRW had strong support. Panel B shows that for simulated TLWs only the LW and TLW had strong support.

Appendix B

Description of the test of absolute fit

When trying to identify the process producing a movement pattern it is important to perform a test of absolute fit (Chapter 2). As mentioned in Chapter 3, the G-test was suggested as the test of absolute fit for Lévy strategy studies (Edwards, 2011; Edwards et al., 2007). However, this test is inadequate for my method because it assumes that the observations are independent. This assumption is violated in the case of the CCRW as it explicitly models correlation in observations. Therefore, I have modified the original test of absolute fit by applying the G-test to the pseudo-residuals rather than to the observations. In this Appendix, I describe in details my test of absolute fit. I start by describing how I calculate pseudo-residuals. I then describe how they are used in the G-test.

Pseudo-residuals can be interpreted as a type of model residuals that accounts for the interdependence of observations. I used ordinary uniform pseudo-residuals (Zucchini and MacDonald, 2009), which are defined as:

$$u_t = Pr(D_t \leq d_t) = F_{i_t}(d_t), \tag{B.1}$$

where d_t is the observation associated with the step at time t and F_{i_t} is the cumulative distribution function (CDF) of d_t under the model of interest, i, at the MLE. In the case of all models except the CCRW, F_{i_t} remains constant for all time steps and can thus be simplified to F_i. For the CCRW, F_{i_t} changes at each time step and incorporates the dependence of the observation at time t, d_t, on all other observations,

$\boldsymbol{d}^{(-t)} = (\boldsymbol{l}^{(-t)}, \boldsymbol{\theta}^{(-t)})$, (Zucchini and MacDonald, 2009):

$$u_t = Pr(D_t \leq d_t | \boldsymbol{D}^{(-t)} = \boldsymbol{d}^{(-t)}) = F_{i_t}(d_t) \tag{B.2}$$

$$= \frac{\boldsymbol{\delta P}(d_1)\ \prod_{s=2}^{t-1} (\boldsymbol{\Gamma P}(d_s))\ \boldsymbol{\Gamma Q}(d_t)\ \prod_{z=t+1}^{n} (\boldsymbol{\Gamma P}(d_z))\boldsymbol{1}}{\boldsymbol{\delta P}(d_1)\ \prod_{s=2}^{t-1} (\boldsymbol{\Gamma P}(d_s))\ \boldsymbol{\Gamma}\ \prod_{z=t+1}^{n} (\boldsymbol{\Gamma P}(d_z))\boldsymbol{1}} \tag{B.3}$$

where $\boldsymbol{\delta}$ is the initial probability vector as defined by Eqn. 3.4, $\boldsymbol{P}(d_t)$ is the observation probability matrix as defined by Eqn. 3.6, $\boldsymbol{Q}(d_t)$ is the cumulative distribution matrix as defined below in Eqns. B.4 and B.5, $\boldsymbol{\Gamma}$ is the transition probability matrix as defined by Eqn. 3.3, and $\boldsymbol{1}$ is a column vector of ones.

To simplify the analysis, I calculate the pseudo-residuals independently for the step length, l_t, and the turning angle, θ_t. Thus for each model I have two separate definition of F_{i_t}. Each of these definitions of F_{i_t} is either one CDF, or a weighted combination of CDFs in the case of the CCRW. In the cases where I did not find a simple CDF, I numerically integrated the PDF of the model of interest from the minimum possible value to the observed value. For the CCRW, I defined two different CDF matrices, one for the step length:

$$\boldsymbol{Q_l}(l_t) = \begin{pmatrix} \Phi(l_t | \lambda_{\mathrm{I}}, a) & 0 \\ 0 & \Phi(l_t | \lambda_{\mathrm{E}}, a) \end{pmatrix}, \tag{B.4}$$

and one for the turning angle:

$$\boldsymbol{Q_\theta}(\theta_t) = \begin{pmatrix} V_0(\theta_t) & 0 \\ 0 & V(\theta_t | \kappa_{\mathrm{E}}) \end{pmatrix}. \tag{B.5}$$

In both cases, the elements of $\boldsymbol{Q}$ are the cumulative distribution functions of the observation probabilities (Eqns. 3.1 and 3.2) associated with the appropriate measure.

By definition, the uniform pseudo-residuals, u_t, are uniformly distributed (Zucchini and MacDonald, 2009) and to verify the absolute fit of the model, I performed a G-test (Sokal and Rohlf, 1981) that compares the distribution of the pseudo-residuals to the uniform distribution. To do so, I discretise both the expected and the observed distributions of the pseudo-residuals. To reduce the potential bias associated with bins that have small expected values (Sokal and Rohlf, 1981), I discretise the distributions into equal size bins so each had an expected value of approximately 10 pseudo-residuals and I use William's correction. The degrees of freedom, df, of the G-test depends on the number of bins, c, and the number of parameters estimated, k: $df = c - k - 1$. As I was estimating the pseudo-residuals of the step length and the turning angle independently

I only included the parameters associated with each of these measures, which was at maximum 3. This means that to get $df > 0$, a minimum of 5 bins was needed. As each bin had a minimum of 10 expected values, a minimum of 50 steps was needed to perform this test of absolute fit.

Because I am calculating the pseudo-residuals independently for the step length and the turning angle, I apply the G-test to each set of pseudo-residuals independently. I subsequently combined the p-value of the G-test for the step length and the turning angle using Fisher's method (Quinn and Keough, 2002; Sokal and Rohlf, 1981). This method of combining p-values is for independent tests (Quinn and Keough, 2002). This is violated in the case of the CCRW (see eq. B.3), and thus this method only approximates the overall p-value. The simulation results presented in Chapter 3 indicate that such approximation is adequate. In particular, the similarity between the rejection rates of the CCRW (0.062) and the TLW (0.065) suggests that the violation of the assumption of independence specific to the CCRW results in no obvious bias compared to the TLW.

Note that the combined p-value can be inappropriate when the movement path is processed using methods such the local turn method to identify biologically relevant steps, especially when the threshold angle is large. The reason is unrelated to statistical independence. Rather, it stems from the fact that while this technique reduces the number small turning angles, none of the models allow for low turning angle frequency at 0. When using this type of techniques, one should also investigate the absolute test of fit that use only the step length pseudo-residuals. I verified whether my empirical results changed if I used only the step length pseudo-residuals. For both bears, the movement paths remained significantly different from the CCRW ($p < 0.01$). The movement path of Bear 1 also remained significantly different from the TCRW ($p < 0.01$).

Appendix C

Variation in threshold angle

In Chapter 4, I used a threshold angle of 10° to estimate biological relevant steps out of the sampled steps. In this Appendix I show that the results remain largely unchanged when other threshold angles are used. As mentioned in Chapter 4, I used the local turn definition to identify significant turns (Codling and Plank, 2011; Reynolds et al., 2007). This method creates a step by amalgamating any consecutive sampled steps that have a turn angle in any direction smaller than the threshold angle (Fig. C.1). Thus under the significant turns definition a new step is started every time a turn angle, as defined by the sampling time interval, is greater or equal to the threshold angle. There are two additional cases that can results in the start of a new step. The first is associated with locations of an animal that did not move. As a pause in movement is a clear sign of the end of biologically relevant step, consecutive locations that have exactly the same coordinates are considered a feature used to identify the ending location of a step. The "steps" between such locations are removed from the time-series and a new step is started with the last of the series of locations with the same coordinates. The second is associated to missing locations. Although missing locations can be handled by the models, the occurrence of missing locations affects steps defined by significant turns. There are two alternative methods to handle missing locations when creating steps defined by significant turns. One alternative is to ignore the missing locations and calculate the step based on the locations before and after the missing location. The other is to stop the step at the location before the missing location and start a new step after the missing location. I chose to use the second method because the first might misrepresent the movement during the missing locations. Note however that the second option will potentially break down long moves. Because missing locations could potentially impact the analyses, I restrained my analyses to movement paths that had < 30% of the location missing. Fig. C.2 demonstrates the impact of variation in threshold angle and missing locations on a movement path.

To look at the impact of the threshold angle on the results, I have reapplied the models to my data using threshold angles ranging from 0 – 60°. Using a threshold angle of 60° includes as forward movement the third of a circle. I constrained the analysis to movement path with at least 50 steps and with < 30% of the location missing for all threshold angles investigated. This ensured that the analyses with different threshold angle included the same individuals and thus were comparable. Because movement paths defined using high threshold angles have fewer steps, this constraint resulted in a reduced data set compared to the one presented in Chapter 4.

Increasing the threshold angle decreased number of paths that have the CCRW as their best model and increased number of paths that have the TLW and the TBW as their best model (Table C.1). While increasing the threshold angle resulted in seven movement paths to change from CCRW to TBW, only one changed from CCRW to TLW (Fig. C.2). The mean Akaike weight for the CCRW remained high for all threshold angles, with its lowest value being 0.88 (Table C.1). Regardless of the threshold angle used, some movement paths were not significantly different from the CCRW. If the threshold angle resulted in paths having the TLW as their best model, the mean Akaike weight for the TLW was 1.00. However, all movement paths remained significantly different from TLW (Table C.2). As for the results presented in Chapter 4, when only the TLW and TBW were considered as alternatives there was substantial support for the TLW (Table C.2). Such support increased with increasing the threshold angle.

Using the threshold angle impacted the test of absolute fit. When the sample steps were used (threshold angle is 0°), the tests that included both the distribution of the step lengths and turning angles were similar to those that used only the step length distribution (Table C.1). Including the turning angle distribution in the absolute test of fit of movement path with high threshold increased the rejection rate of the test of absolute fit (Table C.1). This is not surprising. The local turn method removes small turning angles, but none of the models allow for low turn angle frequency at 0°. This is why I only present the test that used the step length distribution in Chapter 4. As the sample size is also likely to impact the rejection rate of the test of absolute fit I present the relationship between the sample size and *p*-value in Fig. C.3.

Table C.1: Relative and absolute fit of models when different threshold angles are used to define biologically relevant steps. For each model, I present the number of movement paths selected as best model, their mean Akaike weight, and how many of them are not significantly different from this model when both step lengths and turn angles are included, and in bracket when only the step lengths are considered. My dataset included the movement paths of 22 caribou, 20 grizzly bears, and 11 polar bears.

Threshold angle (°)	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
0	CCRW	20	20	11	0.96	1.00	1.00	11(11)	8(7)	0(0)
	TLW	0	0	0	–	–	–	–	–	–
	TBW	2	0	0	0.65	–	–	0(0)	–	–
	TCRW	0	0	0	–	–	–	–	–	–
10	CCRW	21	20	11	0.92	1.00	1.00	9(9)	0(5)	0(0)
	TLW	0	0	0	–	–	–	–	–	–
	TBW	1	0	0	0.61	–	–	0(1)	–	–
	TCRW	0	0	0	–	–	–	–	–	–
20	CCRW	21	20	11	0.92	1.00	1.00	5(14)	0(6)	0(0)
	TLW	0	0	0	–	–	–	–	–	–
	TBW	1	0	0	0.68	–	–	0(0)	–	–
	TCRW	0	0	0	–	–	–	–	–	–
30	CCRW	21	20	11	0.90	0.98	1.00	0(12)	1(7)	0(1)
	TLW	0	0	0	–	–	–	–	–	–
	TBW	1	0	0	0.71	–	–	0(0)	–	–
	TCRW	0	0	0	–	–	–	–	–	–
40	CCRW	21	19	11	0.90	1.00	1.00	0(11)	0(10)	0(1)
	TLW	0	1	0	–	0.98	–	–	0(0)	–
	TBW	1	0	0	0.73	–	–	0(0)	–	–
	TCRW	0	0	0	–	–	–	–	–	–
50	CCRW	18	19	11	0.88	1.00	1.00	0(10)	0(9)	0(0)
	TLW	0	1	0	–	1.00	–	–	0(0)	–
	TBW	4	0	0	0.60	–	–	0(2)	–	–
	TCRW	0	0	0	–	–	–	–	–	–
60	CCRW	15	19	11	0.94	0.99	0.99	0(6)	0(9)	0(1)
	TLW	0	1	0	–	1.00	–	–	0(0)	–
	TBW	7	0	0	0.59	–	–	0(6)	–	–
	TCRW	0	0	0	–	–	–	–	–	–

Table C.2: Relative and absolute fit of the two models generally used in Lévy walk analysis when different threshold angles are used to define biologically relevant steps. For each model, I present the number of movement paths selected as best model with AIC_c and the mean Akaike weight of these selected paths. I also present how many of the overall paths are not significantly different from the TLW and TBW when only the step lengths are considered. My dataset included the movement paths of 22 caribou, 20 grizzly bears, and 11 polar bears.

Threshold angle (°)	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
0	TLW	0	10	1	–	0.97	1.00	0	0	0
	TBW	22	10	10	1.00	1.00	1.00	10	0	0
10	TLW	0	9	1	–	1.00	1.00	0	0	0
	TBW	22	11	10	1.00	0.99	1.00	11	0	0
20	TLW	0	9	1	–	1.00	1.00	0	0	0
	TBW	22	11	10	1.00	0.97	1.00	8	0	0
30	TLW	0	11	2	–	0.99	1.00	0	0	0
	TBW	22	9	9	1.00	0.98	1.00	9	0	0
40	TLW	0	12	2	–	1.00	1.00	0	0	0
	TBW	22	8	9	1.00	1.00	1.00	9	2	0
50	TLW	0	13	2	–	0.99	1.00	0	0	0
	TBW	22	7	9	1.00	0.94	1.00	11	1	0
60	TLW	0	16	2	–	0.98	1.00	0	0	0
	TBW	22	4	9	1.00	1.00	1.00	11	1	0

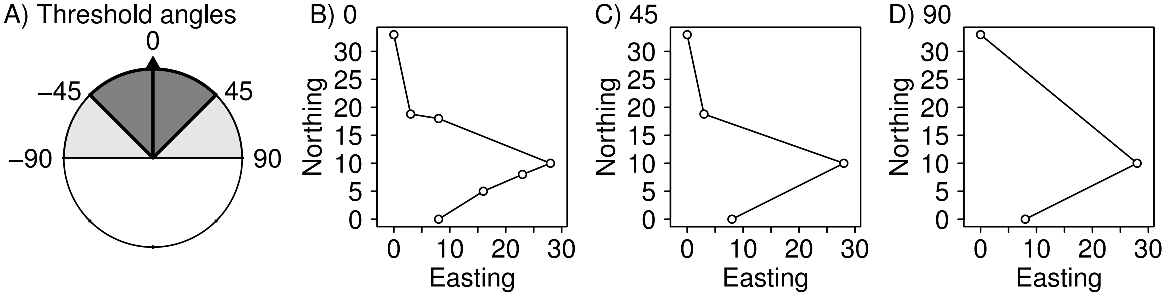

Figure C.1: Transforming steps defined by regular time intervals into biologically relevant steps using the local turn method. (A) Representation of three different threshold angles. The arrow depicts the direction of the previous step. (B) Movement path with five steps as defined by regular time intervals, which correspond to a threshold angle of 0°. (C-D) The same movement path when defined by significant turns with a threshold angle of 45-90°.

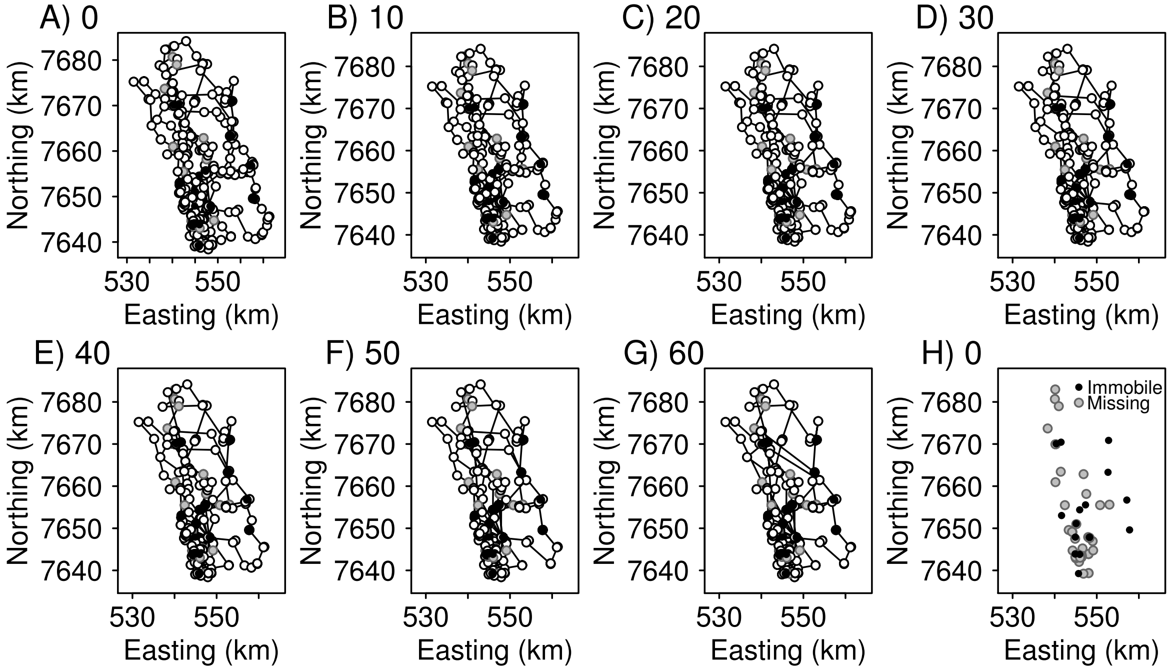

Figure C.2: Movement path of one grizzly bear for the threshold angles of: (A) 0°, which is the equivalent to using the sampled steps, (B-H) 10-60°, as indicated in the figure. Panel G shows the locations assigned as immobile and for missing, the last location before a missing location is represented. The best model according to AIC_c is the CCRW for threshold angles 0-30° and TLW for threshold angles 40-60°.

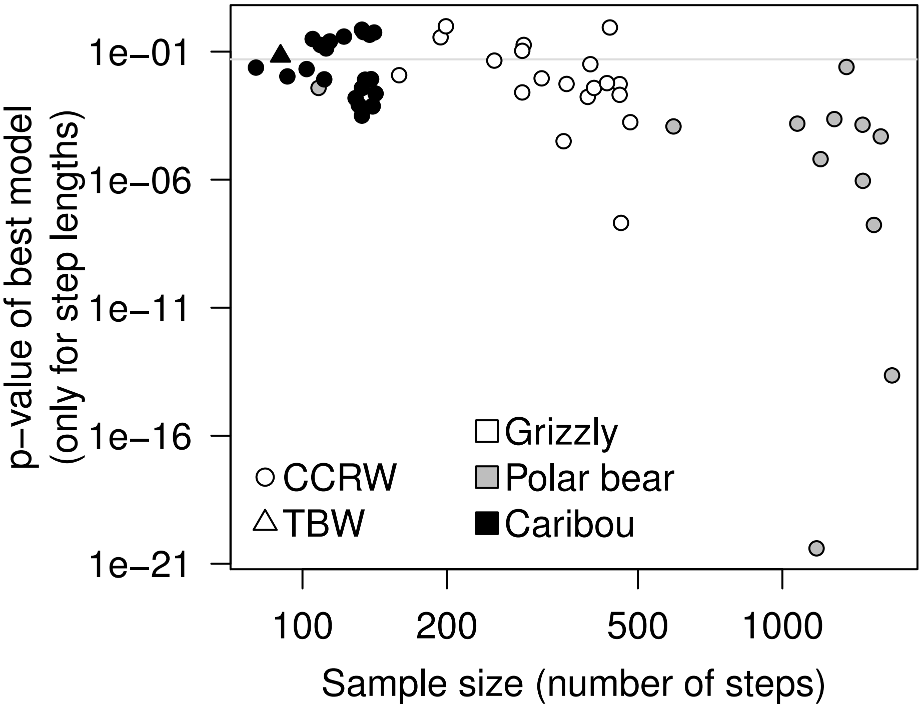

Figure C.3: Relationship between the absolute fit of the best model and the size of movement paths. The *p*-values are based solely on step lengths. The color of symbols represents the species, while their shape represents the model selected as best. The gray line indicates the critical value used for the analyses: $\alpha = 0.05$.