

# Energy Selection Functions: Modelling the Energetic Drivers of Animal Movement and Habitat Use

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## **Abstract**

Energetics are a key driver of animal decision-making, as survival depends on the balance between foraging benefits and movement costs. This fundamental perspective is often missing from habitat selection studies, which mainly describe simple correlations between space use and environmental features. To address this gap, we present a new model, the energy selection function (ESF), to assess how moving animals choose habitat based on energetic considerations, thus incorporating a key aspect of evolutionary behaviour into habitat selection analysis. We outline a workflow, from data-gathering to statistical analysis, and demonstrate the model's utility with a case study of polar bears. Our findings show how cost-minimization may arise in species that inhabit environments with an unpredictable distribution of energetic gains. Because of its close links to existing habitat selection models, the ESF is widely applicable to any study system where energetics can be derived, and has immense potential for methodological extensions.

# 1 Introduction

Foraging and movement are core considerations in animal ecology that reflect fundamental aspects of energetic balance and optimality. Animals should distribute themselves in space so as to maximize their access to energetically rich resources, while minimizing the costs of travel associated with foraging (Emlen, 1966; Pyke *et al.*, 1977; Pyke, 2019). Therefore, energetic balance is a critical component of optimal foraging theory, which assumes that foraging animals should maximize their net energy intake. Theories of how animals search for and distribute themselves relative to food range from random search strategies (Viswanathan *et al.*, 1999; Bartumeus & Catalan, 2009) to cognitively-based movement decisions (Charnov, 1976; Pyke *et al.*, 1977; Pyke, 2019). Models based on these theories are therefore inherently based on assumptions that animals have either no knowledge (e.g., Lévy foraging) or perfect knowledge (e.g., cognitive foraging theory) of their environmental surroundings and internal state (Pyke, 2015, 2019). In reality, animals' knowledge will typically sit between these two extremes. To further the biological realism in modelling animal space use, there has been increased interest in the mechanistic processes of foraging movement (Nathan *et al.*, 2008; Pyke, 2019). While these models have considered the role of memory and perception in foraging (Van Der Post & Semmann, 2011; Bonnell *et al.*, 2013), attempts to estimate the direct energetic consequences of movement decisions are still rare. Energy-based models could provide a crucial link between movement and foraging ecology, uniting them under a common bioenergetic paradigm.

Optimal foraging research often focuses on the energetic benefits of movement and space-use patterns. These studies describe foraging strategies in a patchy environment, and examine prey and patch selection based on factors such as travel time, perception, and memory (Charnov, 1976; Van Der Post & Semmann, 2011; Bonnell *et al.*, 2013). To assess food preference, habitat selection models often include covariates that represent foraging potential. These covariates are usually approximate measures of forage quality or resource availability (e.g., Bastille-Rousseau *et al.*, 2020), but may not be proportional to energetic benefits. Even in cases with more realistic depictions of energy intake (e.g., the energetic profitability of resources combined with biomass; Fortin *et al.*, 2003), the role of energetic costs is still often unquantified. Therefore, although these studies have been instrumental to understand resource preference, new models with realistic depictions of energy could be useful to fully examine the mechanisms of animal space use.

When considered in a foraging context, energetic costs are often assumed to increase linearly with time and/or distance (Reynolds, 2013). In reality, the costs vary widely depending on factors such as mode of transport (Nathan *et al.*, 2008; Griffen, 2018) and environmental conditions (e.g., topography, weather,

substrate; Crête & Larivière, 2003; Wilson *et al.*, 2012). Energy landscapes have been developed as a method to evaluate environmentally-varying movement costs, which can be combined with animal movement data (Wilson *et al.*, 2012; Shepard *et al.*, 2013; Gallagher *et al.*, 2017). Environmental variables, such as air velocity for birds (Shepard *et al.*, 2013), water depth for diving animals (Wilson *et al.*, 2012), or habitat type (Pagano *et al.*, 2020), may be considered in cost estimations. Since energy landscapes are based on spatiotemporal environmental data, these models quantify the energetic costs of moving through heterogeneous or dynamic environments and could be powerful if combined with foraging theory.

To link foraging and movement, optimality models should quantify both the energetic costs and gains of movement decisions. Despite long-standing interest in cost-benefit functions (Schoener, 1971; Sih, 1984), there have been few attempts to energetically compare movement costs to the associated nutritional benefits (Nathan *et al.*, 2008; Owen-Smith *et al.*, 2010). As foraging theories are ultimately interested in energy, we propose using bioenergetics as a unifying currency in movement decision-making. With this approach, we can assess the relative contribution of energetic gains and costs to observed movements. Animals may make movement decisions primarily based on the need to maximize energy intake, minimize energy use, or balance the two (Schoener, 1971; Shepard *et al.*, 2009; Cornioley *et al.*, 2016). By examining energetics at the scale of movement steps (i.e., movements between successive recorded locations), we can link movement ecology to its energetic drivers, allowing us to assess support for foraging theories. We can therefore gain insights into how energetic trade-offs give rise to movement and space-use.

In this paper, we introduce a method that explicitly considers movement and habitat selection in an energetic context. In a model we term an energy selection function (ESF), we evaluate preference for energetic covariates, representing energy gain and energy expenditure. We describe the methodological links to resource and step selection functions (RSFs, SSFs), while showing how the ESF is conceptually unique in its treatment of movement and habitat availability. We provide practical guidance to implement the ESF and define covariates, verify the inference procedure through simulations, and provide an example case study of polar bears (*Ursus maritimus*) in the Beaufort Sea, Canada.

## 2 The ESF

### 2.1 ESF Model Formulation

We first present standard habitat selection models (RSFs, SSFs) from which we base the ESF. To estimate habitat preference, these models employ a use-availability approach, in which we contrast where the animal

went (i.e., what resources they used) with where they could have gone (i.e., available habitat) (Manly *et al.*, 2002; Fortin *et al.*, 2005). While RSFs assess habitat selection at the scale of the utilization distribution (Manly *et al.*, 2002), SSFs are used to analyze autocorrelated animal tracking data and describe resource preference at the scale of the observed movement step (Fortin *et al.*, 2005; Forester *et al.*, 2009; Thurfjell *et al.*, 2014). SSFs consider that movement constraints limit the habitat availability of an RSF, and give the likelihood of a movement step ending at location  $y$  given that it started at location  $x$  in the study region  $\Omega$  as

$$f(y|x) = \frac{\Phi(y|x)w(x,y)}{\int_{z \in \Omega} \Phi(z|x)w(x,z)dz}. \quad (1)$$

Following Forester *et al.* (2009), we consider the numerator to be the SSF. The first term,  $\Phi(y|x)$ , is the resource-independent movement kernel, which describes how an animal would move in a homogeneous landscape or in the absence of resource preference (Forester *et al.*, 2009). The second term,  $w(x,y)$ , is a weighting function and represents resource selection without movement constraints. The weighting function is typically defined as a log-linear model:  $w(x,y) = \exp\{\beta \cdot H(x,y)\}$ , where  $\beta$  is a vector of parameters representing the strength of selection for  $H(x,y)$ , a vector of habitat covariates. It can also include variables that correct for any errors in estimating  $\Phi(y|x)$  (Avgar *et al.*, 2016). Therefore, by assuming the step density to be a product of resource selection  $w(x,y)$  and movement  $\Phi(y|x)$ , SSFs consider the effect of environmental covariates on short-term movement decisions. The denominator of Equation 1 is a normalization constant that ensures the SSF likelihood is a probability density function with respect to  $y$  (Forester *et al.*, 2009; Potts *et al.*, 2014). The likelihood can be optimised with respect to  $\beta$ , over all steps, to estimate the set of parameters that maximise the likelihood of an animal selecting the used locations relative to the rest of the available habitat.

We present the ESF as an energy-based habitat selection model. The mathematical formulation is similar to a standard SSF, and it employs many of the same modelling approaches. Broadly, the ESF can be viewed as a special case of SSF, where the resource independent movement kernel is uniform over the whole study region, and where the covariates are based on energetic currencies. The ESF defines the likelihood of a step ending at location  $y$  given that it started at location  $x$  as

$$f(y|x) = \frac{w(x,y)}{\int_{z \in \Omega} w(x,z)dz}, \quad (2)$$

where  $\Omega$  is the study region, and with energy preference modelled as,

$$w(x, y) = \exp\{\beta_1 G(x, y) - \beta_2 C(x, y)\}. \quad (3)$$

We hereafter refer to equation 3 as the ESF, where  $G(x, y)$  and  $C(x, y)$  refer to the energetic gain and energetic cost of the step, respectively. These energetic covariates replace the typical habitat covariates  $H(x, y)$  used in SSFs, allowing us to make inferences about the role of energy in shaping movement. In section 2.3, we explain how energetic covariates can be derived from various types of telemetry and environmental data. In this form,  $\beta_1$  represents the selection for energetic gains  $G(x, y)$ , which may be formulated in terms of energetically beneficial resources, whereas  $\beta_2$  represents the strength of selection against energetic costs, which may reflect avoidance of costly movements and environments. When evaluated together, these parameters provide inferences about different energy maximization strategies in optimal foraging theory.

In the ESF, we do not need to include the resource-independent movement kernel  $\Phi(y|x)$  as a separate term. Rather, since the various aspects of animal movement, such as speed and tortuosity, directly affect energy expenditure (Wilson *et al.*, 2013, 2020), they are therefore accounted for in the cost term,  $C(x, y)$ . We illustrate how movement can be incorporated into  $C(x, y)$  in Figure 1, which shows how energetic gains and costs contribute to the ESF. Thus, similarly to integrated step selection analysis (iSSA; Avgar *et al.*, 2016), the ESF can be viewed as evaluating movement and habitat selection simultaneously.

## 2.2 Implementation

Consider a movement track  $\{x_1, x_2, \dots, x_n\}$  collected at regular time intervals. The ESF defines the likelihood of the entire track as  $L(\beta_1, \beta_2 | x_1, \dots, x_n) = \prod_{i=1}^{n-1} f(x_{i+1}|x_i)$ , where  $f(x_{i+1}|x_i)$  is the likelihood of a single step (equation 2). However, it can be computationally demanding to calculate the exact likelihood, as this would require evaluation of  $w$  over the entire domain of integration  $\Omega$  (i.e., continuously over the whole study region). In practice, we can approximate this likelihood using a case-control design (Forester *et al.*, 2009; Thurfjell *et al.*, 2014). For each observed location  $x_i$  (hereafter, a case), we generate a set of random locations (hereafter, controls) which represent a sample of the available habitat. Using Monte Carlo integration over the control locations  $\{z_{i1}, z_{i2}, \dots, z_{iK}\}$ , we calculate the approximate likelihood as

$$\tilde{L}(\beta_1, \beta_2 | x_1, \dots, x_n) = \prod_{i=1}^{n-1} \frac{w(x_i, x_{i+1})}{\sum_{k=0}^K w(x_i, z_{ik})}, \quad (4)$$

where we define  $z_{i0} = x_{i+1}$ .

In theory, we should generate control locations  $\{z_{i1}, z_{i2}, \dots, z_{iK}\}$  uniformly across the whole habitat,  $\Omega$ . This procedure would be computationally intense, but it can be improved by noticing that the ESF (Equation 3) will typically take small values over most of  $\Omega$ . That is, the properties of energetic costs ensure that the ESF decays as a function of the distance to the start point of the step  $x_i$ . It is therefore sufficient to evaluate the ESF over a neighbourhood of the start point to obtain a good approximation of the likelihood, and we suggest generating control locations uniformly on a disc around  $x_i$  (see Appendix A for details). The radius  $R$  of the disc needs to be large enough such that the probability of the animal moving beyond  $R$  is negligible. This sampling is not a model of movement or availability, unlike SSFs where controls are distributed according to  $\Phi(y|x)$ . Here, we suggest using control locations over a disc merely for computational convenience, and in the ESF framework, the availability is determined by the effect of energetic costs on movement. This can be viewed as a special case of importance sampling, to increase the precision of the Monte Carlo integration. In principle, the control locations do not need to follow a uniform distribution (e.g., they could be normally distributed around the start point  $x$ ) but, in such a case, the probability density function of that distribution would need to be included as a correction in the denominator of Equation 4.

Given that the ESF uses the same general formulation and case-control design as SSFs, model fitting can be done using the same statistical techniques and software. We can estimate  $\beta_1, \beta_2$  with maximum likelihood estimation (MLE), with regards to equation 4. MLE is fast and accessible, using numerical optimizers (e.g., *optim* in R) or existing software for conditional logistic regression (e.g., the R function *clogit*, package *survival*). The ESF may be appealing to practitioners, as it builds on existing models and can be implemented with common, accessible software and techniques. In Appendix B, we verify these implementation methods with a short technical simulation, which showed accurate inferences under different levels of spatial autocorrelation and number of control locations used (Figure S4).

## 2.3 Defining the Energetic Covariates

The ESF is applicable to any system where there is adequate energetic data, and the covariates must be formulated specifically to each study.  $G$  (gains) and  $C$  (costs) should be in energetic terms (i.e., proportional), although not necessarily in standard units (e.g., kJ). Here, we focus on foraging resources and movement, but the approach can be extended if other environmental factors (e.g., temperature, weather) are important to energy gain or expenditure. We provide general recommendations, but in practice, covariate definitions should be largely based on available ecological knowledge and data of the study system.

Energetic gains mainly arise from the consumption of energetically beneficial resources, whose distribution

can be derived from environmental data (e.g., NVDI, prey or vegetation biomass; Fortin *et al.*, 2003; Pilfold *et al.*, 2014). Metrics should contain relevant information to represent consumable and digestible biomass, and more than one resource can be incorporated into  $G$  if they are weighted based on their energetic contribution. Further, resources may be combined with movement data, in cases with strong empirical or hypothesized relationships between foraging potential and movement speed (Figure S5). Under this formulation, we can evaluate selection for foraging resources as an energetic currency, rather than preference for individual resources.

Energetic costs should be formulated primarily in terms of movement (tortuosity speed; Taylor *et al.*, 1970; Wilson *et al.*, 2013), which can be quantified from geographical positioning system (GPS) location data. To inform the costs of movement steps, GPS metrics can be combined with captive studies (e.g., treadmills; Bidder *et al.*, 2017) and field measures that more directly measure energy expenditure and behaviour (e.g., doubly-labelled water, heart rate, dynamic body acceleration (DBA); Butler *et al.*, 2004; Pagano & Williams, 2019; Wilson *et al.*, 2020). The cost of movement is also affected by habitat factors, such as substrate penetrability (soft vs. hard; Crête & Larivière, 2003), slope (Halsey, 2016), and resistivity (e.g., wind and water currents; Chapman *et al.*, 2011; Shepard *et al.*, 2013). Therefore, habitat features and movement data can be combined into a synthetic model of energy expenditure (see Section 3, Figure S5) or correlated to estimate the energetic costs of control steps.

### 3 Case Study

Polar bears are sea ice-obligate apex carnivores that forage on fat-rich prey, such as ringed seals (*Pusa hispida*) and bearded seals (*Erignathus barbatus*) (Pilfold *et al.*, 2012). Polar bear abundance, distribution, and body condition are associated with the spatial and temporal distribution of their prey (Pilfold *et al.*, 2014; Galicia *et al.*, 2020), as well as the sea ice habitat configuration (Lunn *et al.*, 2016; McCall *et al.*, 2016). Energy gain is highest in the spring when bears enter a hyperphagic period (Pilfold *et al.*, 2012), before fasting for several months (Stirling & Øritsland, 1995). Therefore, polar bears have limited time to store enough energy to survive and reproduce (Stirling & Øritsland, 1995), and must balance the high-energy returns of their prey against energetic costs. Polar bears have energetically expensive locomotion (Hurst *et al.*, 1982a; Pagano *et al.*, 2018) that is affected by habitat dynamics, including sea ice drift (Durner *et al.*, 2017; Klappstein *et al.*, 2020) and fragmentation (Blanchet *et al.*, 2020). To reach or remain in preferred habitat, polar bears may oppose the moving sea ice and expend more energy to cover the same geographic distance (Mauritzen



*et al.*, 2003; Auger-Méthé *et al.*, 2016; Durner *et al.*, 2017). Further, when sea ice cover is low, polar bears are more likely to swim (Pilfold *et al.*, 2016; Lone *et al.*, 2018), which has been estimated to be five times more energetically expensive than walking (Griffen, 2018). These spatiotemporal interactions suggest that energetic considerations may be important in governing polar bear movement and habitat selection.

The energetics of free-ranging polar bears have yet to be analyzed in a framework that considers selection of gains and costs. Movement and habitat selection studies of polar bears often consider environmental conditions with energetic implications without formulating the covariates into an energetic currency (e.g., McCall *et al.*, 2016; Johnson & Derocher, 2020) and/or only including the effect of a single covariate (e.g., Durner *et al.*, 2017; Klappstein *et al.*, 2020). When energetics have been more comprehensively considered, they have been coarsely estimated (e.g., dynamic energy budgets in Molnár *et al.*, 2011) or limited to energetic costs (Blanchet *et al.*, 2020; Pagano *et al.*, 2020). In this case study, we apply the ESF to polar bears in the Beaufort Sea, which has fast ice drift and variable ice concentration (Carmack & Macdonald, 2002). We estimate energetic gains from an energetically-weighted RSF of seal kills, and develop a cost model for use with GPS telemetry data. Therefore, we consider polar bear energetics at the scale of movement-based habitat selection.

## 3.1 Methods

### 3.1.1 Data Processing

We analyzed 4-hour resolution telemetry data from 23 GPS-collared solitary adult ( $> 5$  years old) female polar bears from 2007-2011 in the Canadian Beaufort Sea (Figures 2, S6; Appendix D). We calculated body mass from axillary girth and body length measurements (Thiemann *et al.*, 2011). We omitted GPS locations from dropped collars or deceased bears, following Togunov *et al.* (2020). We defined a movement burst as a sequence of locations with no gaps  $> 24$  hours and only kept bursts with  $\geq 10$  locations. We calculated step length as the Euclidean distance between projected GPS locations (NAD83 UTM Zone 9N, EPSG:3156), and removed unrealistic locations where the step speed was  $> 5.4$  km/h (Whiteman *et al.*, 2015). Then, we imputed missing locations of each burst with a continuous-time correlated random walk model (Johnson *et al.*, 2008), implemented in *momentuHMM* (McClintock & Michelot, 2018). We interpolated relevant environmental variables (described below) with bilinear interpolation (Figure 2), using the *raster* package.

### 3.1.2 Energetic Gains $G$

We derived energetic gains from an RSF model of forage quality from Pilfold *et al.* (2014). The RSF modelled locations of seals killed by polar bears, weighted by biomass, relative to habitat characteristics (see Pilfold *et al.*, 2014). Because the RSF incorporated both seal kill biomass and abundance, we assumed the RSF value to be proportional to energetic return. We extended both the temporal and spatial extent of the original rasters, but not beyond the original range of habitat characteristics and season (Figure 2). We created daily rasters which encompassed approximately 100km off-shore along the coast of Alaska and Canada (from approximately 160°W to 115°W), including the Amundsen Gulf and regions adjacent to Banks Island from March-June of 2007-2011. The resolution of the rasters was 6.25km and RSF values were zero in locations where sea ice was absent.

### 3.1.3 Energetic Costs $C$

We formulated costs based on the movement costs of captive polar bears, combined with environmental covariates to better represent field conditions (Figure 3). Telemetry locations arise from a combination of active bear movement and passive displacement caused by ice drift (Mauritzen *et al.*, 2003; Auger-Méthé *et al.*, 2016; Durner *et al.*, 2017). Therefore, we define a step as the active bear movement between telemetry locations, corrected for ice drift following Klappstein *et al.* (2020), using drift data from the National Snow and Ice Data Center (Polar Pathfinder Daily 25km EASE-Grid Sea Ice Motion Vectors; Tschudi *et al.*, 2019). At each step, a bear can either be swimming or walking on sea ice, which have distinct energetic costs (e.g., Hurst *et al.*, 1982a; Griffen, 2018; Pagano *et al.*, 2018). Using aquatic sensor data from Lone *et al.* (2018), we modelled the relationship between the proportion of time in water and sea ice concentration as a generalized additive model (GAM) in the *mgcv* package (Wood, 2017). Using this curve, we estimated proportion of time spent in water for each polar bear step, which we assumed to be the same as the proportion of the distance travelled (Figures 3, S7). Lastly, we modelled the relationship between travel speed and energy expenditure, using combined estimates from five treadmill studies (Øritsland & Jonker, 1976; Hurst *et al.*, 1982a,b; Watts *et al.*, 1991; Pagano *et al.*, 2018). We modelled energy expenditure as a function of walking speed as a GAM with a gamma response distribution and a positive monotonic constraint in the R package *scam* (Figures 3, S8; Pya & Wood, 2015; Pya, 2019). When the bear was assumed to be walking, the cost was derived directly from this curve, and when the bear was swimming, we multiplied this cost by five to represent the higher energy expenditure (Griffen, 2018). Importantly, our modelling approach estimated similar daily costs as those obtained from doubly-labelled water (Figure S9).

### 3.1.4 Fitting the ESF

We eliminated locations that were outside the spatiotemporal extent of prey data availability (Figures 3, S6). We generated 20 control locations on a disc around each observed location, with radius  $R = 1.1 \times l_m$ , where  $l_m$  is the maximum step length of all observed locations (see Appendix A for justification of  $R$ ). We calculated energetic gains and costs of each step as described above, using environmental covariate values at each end location. We omitted steps from analysis when there were  $> 10$  control locations without an energetic gain estimate (i.e., outside the raster extent). We fit the ESF with the numerical optimizer *optim* separately for each individual bear. We calculated confidence intervals (CIs) based on the approximate standard errors of the maximum likelihood estimates, obtained from the inverse of the Hessian matrix given by *optim*.

## 3.2 Results

We analyzed 7,861 GPS locations (locations per individual: 80–968). Energetic gains at each step (including controls) ranged from 0 to 27.9 (units unknown) and energetic costs ranged from 3.27 to 161 MJ. The median  $\beta_1$  estimate was  $-0.01$  (range  $-0.29, 0.83$ ), with four estimates with CIs that did not overlap zero (Figure 4). Of these, three bears appeared to select for energetic gains ( $\beta_1 \pm 95\% \text{ CI} = 0.83 \pm 0.82$ ;  $0.32 \pm 0.20$ ;  $0.28 \pm 0.17$ ) and only one bear appeared to select against energetic gains ( $\beta_1 \pm 95\% \text{ CI} = -0.29 \pm 0.20$ ). Conversely, all  $\beta_2$  estimates showed a selection against costs, with a median of 0.57 (range 0.32, 0.97), and no CIs overlapped zero for any of the 23 individuals.

## 3.3 Discussion of the Polar Bear Case Study

In this case study, we found a strong pattern of selection against energetic costs in all individuals, but only four showed selection for ( $n = 3$ ) or against ( $n = 1$ ) energetic gains. Since only 4 of 23 estimates showed an effect of gains, it is possible that these could be false positives (Type I error). However, effects may have been hard to detect if the grain size and spatial autocorrelation of our covariate data were too high for the temporal scale and spatial domain size of the telemetry data (Boyce *et al.*, 2003; Boyce, 2006; Northrup *et al.*, 2013). This could result in low variation between case and control locations, particularly if the tracking data is not at a biologically relevant resolution. Future studies should assess the effect of scale on polar bear energy selection. Further, our uncertainty estimates do not consider the error in our covariate data (Pilfold *et al.*, 2014; Tschudi *et al.*, 2019; Togunov *et al.*, 2020), which may affect modelling outcomes (Van Niel &

Austin, 2007). However, error propagation is not standard in habitat selection studies, as methods remain analytically complex and uncertainty in environmental data is often unknown (Molto *et al.*, 2013).

Our results suggest that most solitary female polar bears in the Beaufort Sea employ a cost-minimization strategy. Cost-minimization could arise due to high predictability of energy expenditure, based on internal factors and mechanical movement constraints, while energy-maximization would require polar bears to have knowledge of the unpredictable seal distribution (Ramsay & Stirling, 1986; Ferguson *et al.*, 1999). At the landscape level, polar bear distribution correlates positively to seal kill biomass (Pilfold *et al.*, 2014), but we did not observe this at the scale of the movement step, which may be reflective of local variability in the probability of killing a seal. Further, our model assumes that energy selection is consistent through time and across behaviours, although selection for gains is likely variable over the study period. Polar bears do not enter the main foraging period until mid-April (Pilfold *et al.*, 2012) and continue to gain weight into the summer months (Galicia *et al.*, 2020). From March to May, solitary females may also pair with males for mating, during which they forage less frequently and are sequestered from ideal habitats for up to 18 days at a time (Derocher *et al.*, 2010; Stirling *et al.*, 2016). Additionally, polar bear movements may be influenced by site fidelity (Mauritzen *et al.*, 2001), in which recurrent space-use patterns dominate short-term selection for energetic gains. If selection for gains is affected by competing behaviours, it may be that only individuals with exceptionally strong selection may be identified. These hypotheses should be tested in future research, which may require a more nuanced model formulation, while addressing annual, seasonal, demographic, and spatial variation in energy selection.

## 4 Discussion and Conclusions

Evaluating the energetic basis of animal movement and habitat selection remains a topical issue in ecology (Eisaguirre *et al.*, 2020; Pagano *et al.*, 2020; Williams *et al.*, 2020). Our new model to estimate the energy preferences of animals is similar to recent approaches to combine movement and habitat (Avgar *et al.*, 2016; Michelot *et al.*, 2019), but the ESF uniquely integrates both factors into energetic covariates. Therefore, our approach explicitly accounts for energetics in the selection process. This contrasts with similar work by Eisaguirre *et al.* (2020), which incorporated costs into the availability kernel (so as to ascertain the selection for resources once such costs had been accounted for). In their work, the effect of energetics on movement was treated as a nuisance parameter, rather than the goal of inference. We applied the ESF to lone female polar bears and found that cost-minimization was the most common energetic strategy, which helps explain their

movement in dynamic habitats. We consider this model an important step in uncovering the contribution of energy in observed space use patterns.

The inferences we can make from the ESF necessarily depend on the quality of the estimated energetic variables. Definitions of  $G$  and  $C$  rely on carefully evaluating complex interactions between movement and habitat, and mischaracterization may lead to parameter estimates that do not truly represent energy selection. Although it may not always be possible, defining  $G$  and  $C$  in the same units would facilitate comparison of  $\beta_1$  and  $\beta_2$  (i.e., relative strength of selection) to uncover energetic trade-offs. However, even when the covariates are expressed in different units, we can still make comparisons between individuals or other temporal or demographic factors, as illustrated in Section 3.

Inherently, step selection analyses are sensitive to the spatial and temporal scale of the telemetry and covariate data (Munden *et al.*, 2020). In the ESF, the spatial scale of the energetic covariates should be fine enough that it is possible to observe preference at the scale of the observed movement steps. When covariate data is coarse or spatially autocorrelated, contrast between case and control locations may be low and provide little evidence of selection (Northrup *et al.*, 2013). Another feature of step selection models is that the temporal resolution of the tracking data determines the scale at which the animal’s behaviour is examined (Bastille-Rousseau *et al.*, 2018). For example, selection for foraging resources at the scale of the landscape (as in Section 3) or energy accumulation over a long period (e.g., in the case of kill sites) may not be apparent at the scale of fine-resolution movement steps. The interpretation of the ESF parameters is therefore tied to the time interval of observation, and lack of evidence for selection at the movement step may not translate to a biologically relevant time-scale. Thoughtful programming of telemetry devices, high-frequency data, and continuous-time analogues of SSFs may prove useful to overcome these scale dependencies (e.g., Munden *et al.*, 2020). We hope this study will motivate the collection of more precise data, suited to understand the energetic mechanisms behind animal space use (see Williams *et al.*, 2020, for a review of available technologies).

The ESF has great potential for methodological extensions, due to its close theoretical and practical links to existing methods (SSFs and iSSA). We could add separate terms to the model, such as movement metrics (similar to iSSA; Avgar *et al.*, 2016) or terms with no energetic interpretation. This may prove useful to account for movement when it cannot be included in  $G$  and  $C$  and to assess energetic trade-offs. SSFs have also been used to estimate long-term patterns of space use through simulations (Avgar *et al.*, 2016; Signer *et al.*, 2017). Similarly, it may be possible to generate movement tracks from a fitted ESF to predict the long-term spatial distribution of animals as the result of short-term energy selection. Another possible extension

would be to consider a state-switching ESF model, where an unobserved behavioural state determines the selection parameters for energetic gains and costs. This would allow us to assess behaviour-specific energy selection, and could be written as a hidden Markov model, similarly to the state-switching SSF model of Nicosia *et al.* (2017). Ultimately, the ESF is a widely applicable and flexible method to combine energy, movement, and habitat selection.

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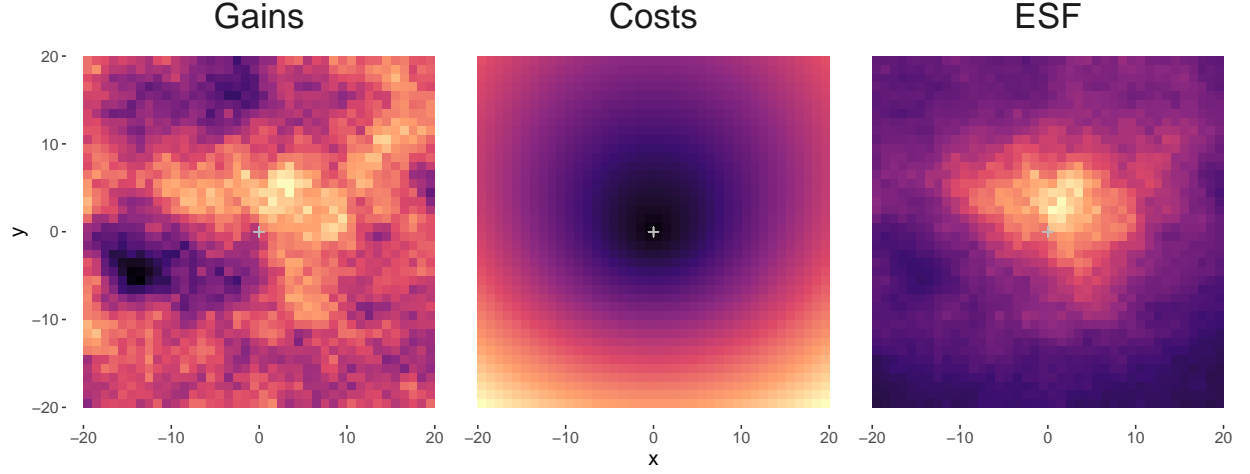


Figure 1: Simulated rasters of energetic gains and energetic costs, and the corresponding ESF. Energetic gains were simulated as a random covariate field and energetic costs were defined as a product of the step length and turning angle from the central location (+), assuming that the animal was facing up the y-axis before turning.  $ESF = \exp(gains - costs)$  to represent optimal movement. In all panels, lighter colours represent higher values.

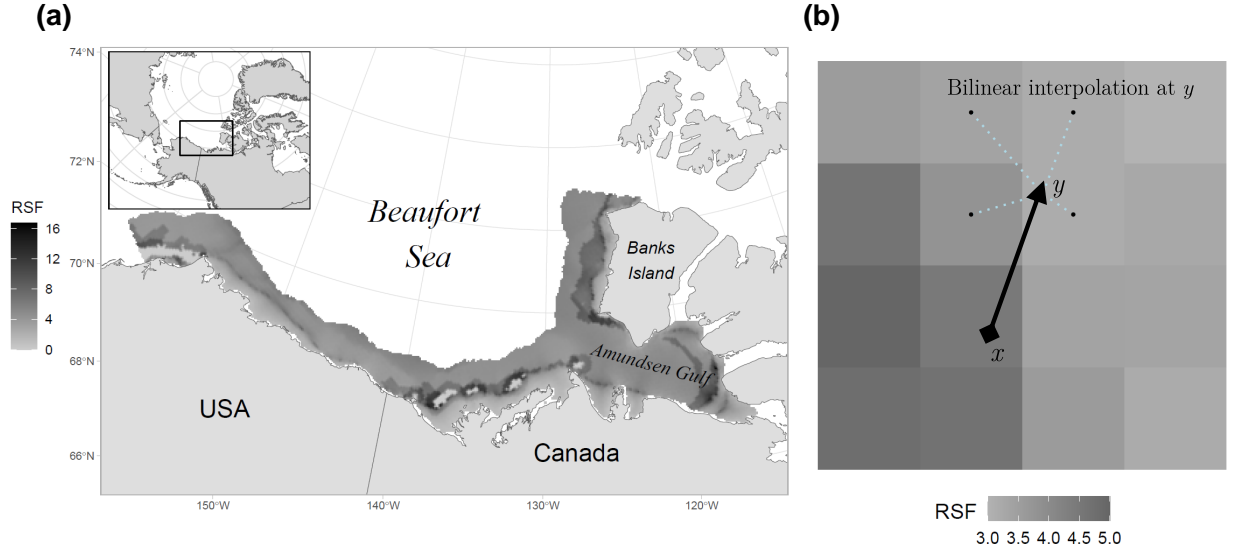


Figure 2: Illustration of energetic gains in polar bear case study. (a) Map of study area overlaid with an example seal biomass RSF (Pilfold *et al.*, 2014). (b) Schematic representation of energetic gain evaluation for a step from  $x$  to  $y$ , using bilinear interpolation at  $y$  based on the four adjacent cells (black dots).

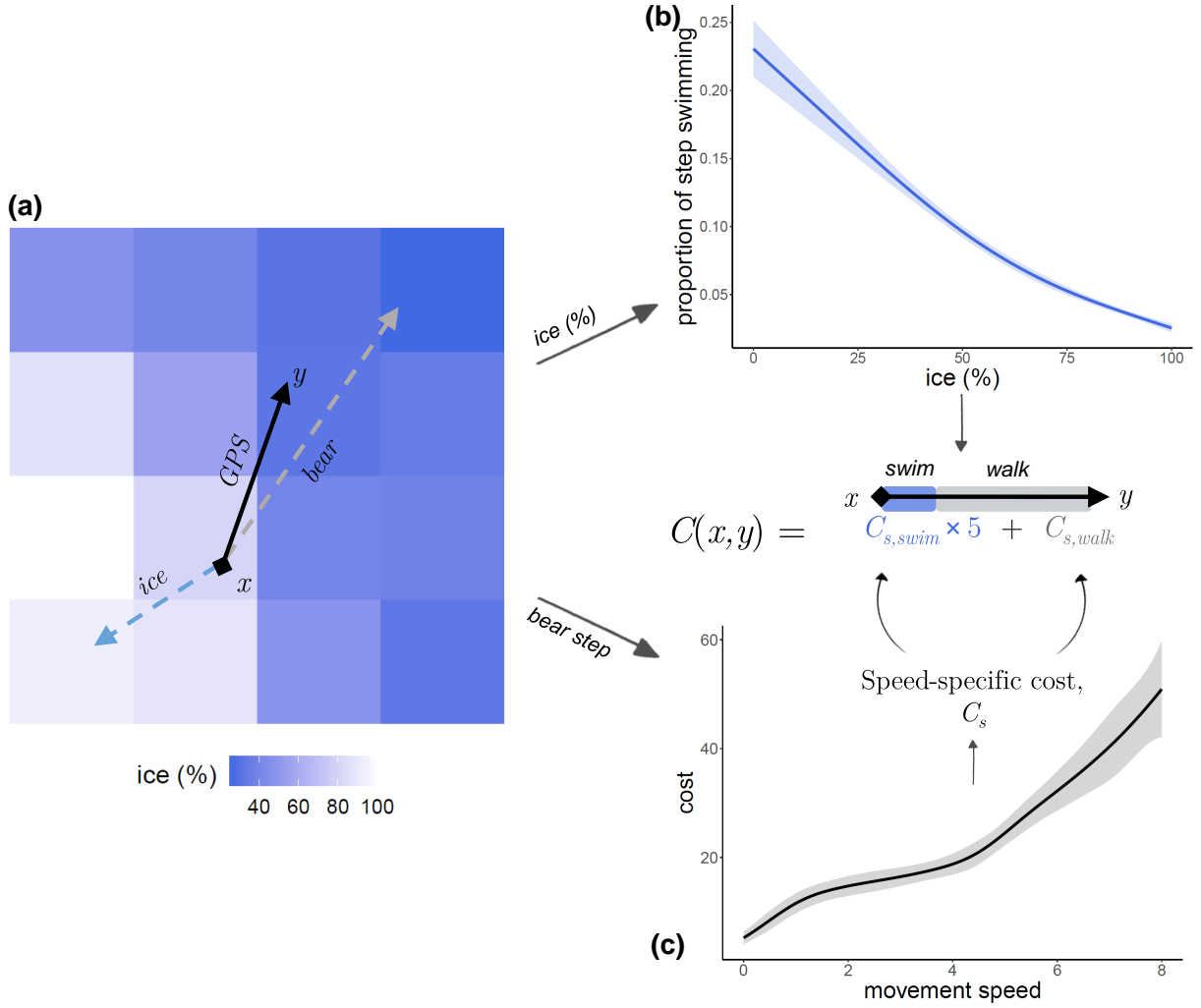


Figure 3: Schematic illustration of energetic cost evaluation in the polar bear case study, for an observed step starting at  $x$  and ending at  $y$ . (a) Arrows represent the observed movement step (black; GPS), ice drift (blue dashed; ice), and actual bear movement (grey dashed; calculated as GPS - ice). Ice concentration (%) is estimated at  $y$  with bilinear interpolation. (b) Modelled relationship between ice concentration and the proportion of the step spent swimming (Lone *et al.*, 2018, ; see Figure S7 for high resolution version). We use the estimated ice % from (a) to estimate the proportion of the bear step spent swimming and walking. (c) Modelled relationship between polar bear movement speed (km/h) and energetic cost (kJ/kg/h) from several treadmill studies (Figure S8 for high resolution version). Using the bear speed and weight, we calculate  $C_s$  for the step.  $C_{s,swim}$  and  $C_{s,walk}$  are  $C_s$  multiplied by the proportion of time in each behaviour. The total energy expenditure of the step  $C(x,y)$  is the sum of  $C_{s,swim}$  multiplied by 5 (to represent the higher costs of swimming) and  $C_{s,walk}$ .

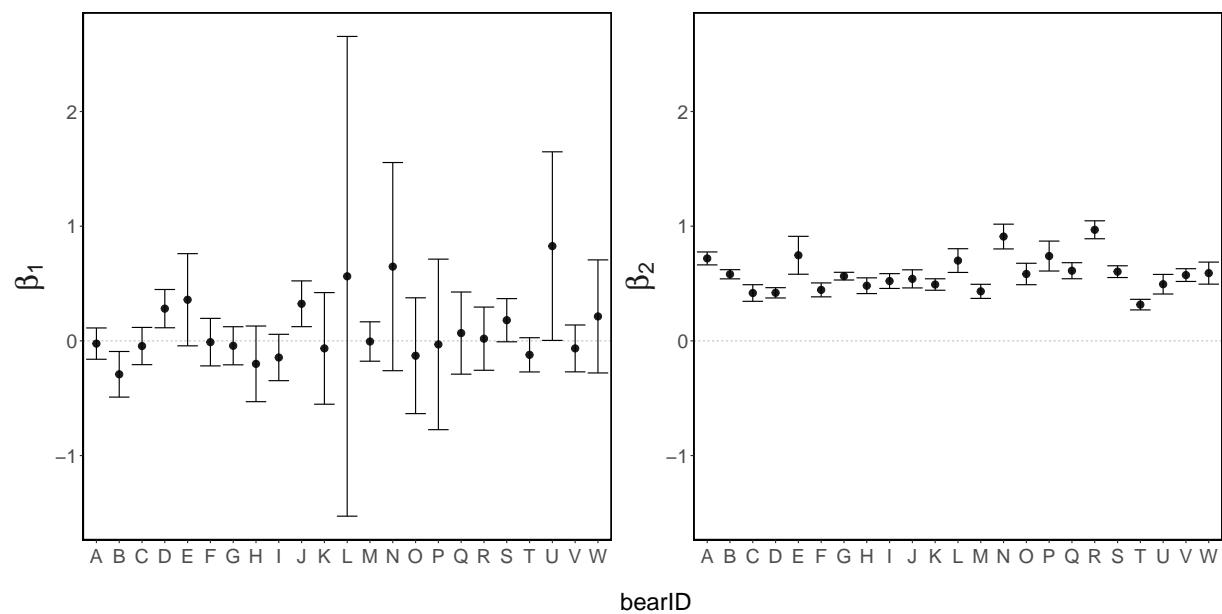


Figure 4: Estimated  $\beta_1$  (selection for gains) and  $\beta_2$  (selection against costs) coefficients of lone adult female polar bears ( $N = 23$ ). Error bars are 95% CIs.