

Energy selection functions: modelling the energetic drivers of animal movement and habitat use

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Short title: Energy selection functions

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Abstract

1. 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 correlations between space use and environmental features, rather than the mechanisms behind these correlations. To address this gap, we present a new modelling framework, the energy selection function (ESF), to assess how moving animals choose habitat based on energetic considerations.
2. The ESF considers that the likelihood of an animal selecting a movement step depends directly on the corresponding energetic gains and costs. The parameters of the ESF measure selection *for* energetic gains and *against* energetic costs; when estimated jointly, these provide inferences about foraging and movement strategies. The ESF can be implemented easily with standard conditional logistic regression software, allowing for fast inference. We outline a workflow, from data-gathering to statistical analysis, and use a case study of polar bears (*Ursus maritimus*) as an illustrative example.
3. We show how defining gains and costs at the scale of the movement step allows us to include detailed information about resource distribution, landscape resistance, and movement patterns.

We demonstrate this in the polar bear case study, in which the results show how cost-minimization may arise in species that inhabit environments with an unpredictable distribution of energetic gains.

4. The ESF combines the energetic consequences of both movement and resource selection, thus incorporating a key aspect of evolutionary behaviour into habitat selection analysis. Because of its close links to existing habitat selection models, the ESF is widely applicable to any study system where energetic gains and costs can be derived, and has immense potential for methodological extensions.

Key words: animal movement, energetics, energy landscapes, habitat selection, movement ecology, optimal foraging theory, polar bear, step selection functions

1 Introduction

Understanding the mechanisms behind the spatial distributions of animals is a core consideration for animal ecology (Kays et al., 2015). Space use patterns are largely driven by the movement decisions made by animals whilst foraging. To increase their chances of survival, animals should distribute themselves in space so as to maximize their access to energetically rich resources, while minimizing the costs of travel (Pyke et al., 1977; Pyke, 2019). Consequently, to uncover the eco-evolutionary reasons behind observed space use patterns requires methods that link space use to optimal foraging decisions, via models of animal movement.

Energy-based models could be an important tool to compare the costs of movement to the associated nutritional benefits. Despite long-standing interest in cost-benefit functions (Schoener, 1971), it remains a challenge to consider both energy expenditure and acquisition in a unified framework (Owen-Smith et al., 2010, but see Hooten et al. 2019). Optimal foraging research often focuses on foraging benefits, using approximate measures of forage quality or resource availability (e.g. Bastille-Rousseau et al., 2020), which may not be proportional to energetic gains. Even in cases with more realistic depictions of energy intake (e.g. the energetic profitability of resources combined with biomass; Fortin et al., 2003), movement costs are often ignored or assumed to increase linearly with time and/or distance (Reynolds, 2013). In reality, the costs vary widely depending on factors such as movement speed (Taylor et al., 1970), mode of transport (Griffen, 2018), and environmental conditions (e.g. topography, weather, substrate; Crête & Larivière, 2003; Wilson et al., 2012). Environmentally-varying movement costs can be quantified in a framework known as an energy landscape, which can incorporate factors 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). Energy landscapes are useful to quantify the energetic costs of moving through heterogeneous or dynamic environments, but have yet to be comprehensively integrated with foraging theory.

Habitat selection models assess how animals distribute themselves in space relative to environmental features, and therefore may be modified to assess the energetic contributions of movement decisions. Resource selection functions have been used to jointly estimate the effects of foraging resources and energetically-costly environmental features on large-scale space-use (Long et al., 2014). However, that approach does not explicitly model movement, and it therefore ignores costs incurred at the scale of the movement step (i.e. movement between successive recorded locations). At this scale, animals may make 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). Although the idea of energy-based movement models is not entirely new,

methods remain analytically complex. For example, Hooten et al. (2019) described a movement model with a binary response “recharge” function (e.g. animals may decide to move to a food patch), based on a latent process for the physiological state of an animal (e.g. its level of satiation or cumulative energy balance). A simpler, yet effective, approach could be to use a movement-based habitat selection model to answer similar questions in a flexible and accessible framework.

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. The ESF has methodological links to resource selection functions (RSFs) and step selection functions (SSFs), and maintains the practical simplicity of use, favouring uptake by ecologists. However, the ESF is conceptually different in defining movement and habitat availability through covariates that can be explicitly linked to energetic trade-offs in decision-making. To demonstrate our approach, we provide practical guidance to implement the ESF and define covariates, and showcase the ESF through an example case study of polar bears (*Ursus maritimus*) in the Beaufort Sea, Canada.

2 The ESF

2.1 ESF model formulation

We present the energy selection function (ESF) as an energy-based habitat selection model, quantifying responses to both energy gain and expenditure. The ESF defines the likelihood of a step ending at location \mathbf{y} given that it started at location \mathbf{x} as

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

where Ω is the study region, the denominator is a normalization constant that ensures the ESF likelihood is a probability density function with respect to \mathbf{y} (Forester et al., 2009; Potts et al., 2014), and with energy preference modelled as,

$$w(\mathbf{x}, \mathbf{y}) = \exp\{\beta_1 G(\mathbf{x}, \mathbf{y}) - \beta_2 C(\mathbf{x}, \mathbf{y})\}. \quad (2)$$

We hereafter refer to Equation 2 as the ESF, where $G(\mathbf{x}, \mathbf{y})$ and $C(\mathbf{x}, \mathbf{y})$ refer to the energetic gain and energetic cost of the step, respectively (Figure 1). In Section 2.4, we explain how these energetic covariates can be derived from telemetry and environmental data. In this form, β_1 represents the selection for energetic

gains $G(\mathbf{x}, \mathbf{y})$, formulated in terms of energetically beneficial resources. β_2 represents the strength of selection against energetic costs $C(\mathbf{x}, \mathbf{y})$, formulated as habitat-specific movement costs. When evaluated together, these parameters provide inferences about different energy maximization strategies in optimal foraging theory, where higher values of either β_1 or β_2 represent strategies to maximize net energy. The likelihood can be optimised with respect to β_1 and β_2 , 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. Ultimately, the ESF can be viewed as a joint model of habitat selection and movement, as captured by selection for gains and against costs, respectively.

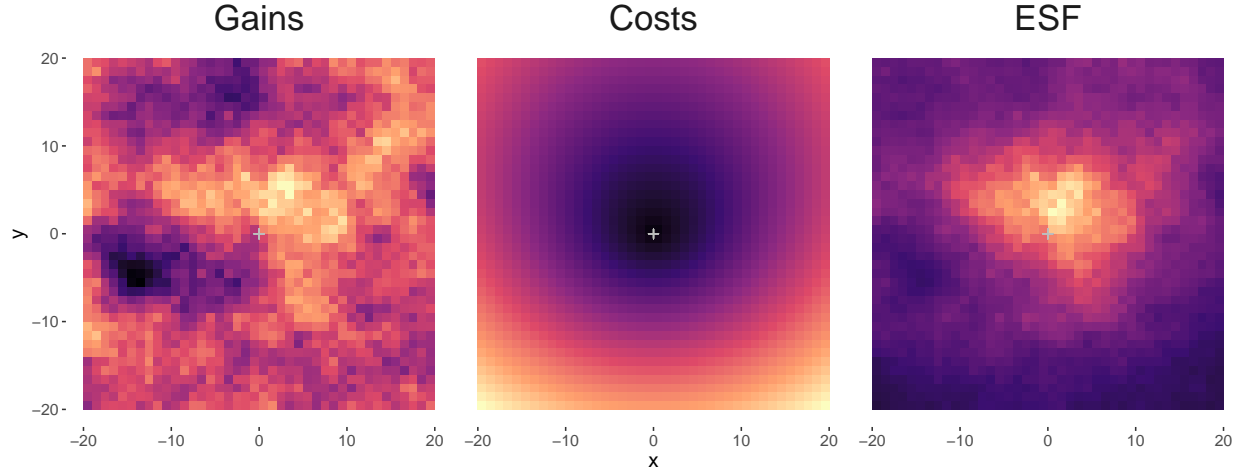


Figure 1: Simulated rasters of energetic gains and energetic costs, and the corresponding ESF. Energetic gains were simulated as a random covariate field and energetic costs were defined as a product of the step length and turning angle from the central location (+), assuming that the animal was facing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

2.2 Comparison to other habitat selection models

The mathematical formulation and modelling approaches of the ESF are similar to those of other common habitat selection models, particularly step selection functions (SSFs). Both models are used to analyse autocorrelated animal tracking data and describe habitat preference at the scale of the observed movement step. SSFs consider that movement constraints limit the habitat availability, and give the likelihood of a movement step ending at location \mathbf{y} given that it started at location \mathbf{x} in the study region Ω as

$$f(\mathbf{y}|\mathbf{x}) = \frac{\Phi(\mathbf{y}|\mathbf{x})w(\mathbf{x}, \mathbf{y})}{\int_{\mathbf{z} \in \Omega} \Phi(\mathbf{z}|\mathbf{x})w(\mathbf{x}, \mathbf{z})d\mathbf{z}}. \quad (3)$$

Following Forester et al. (2009), we consider the numerator to be the SSF. The first term, $\Phi(\mathbf{y}|\mathbf{x})$, 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, $w(\mathbf{x}, \mathbf{y})$, is a weighting function and represents resource selection without movement constraints. The weighting function is typically defined as: $w(\mathbf{x}, \mathbf{y}) = \exp\{\boldsymbol{\beta} \cdot \mathbf{h}(\mathbf{x}, \mathbf{y})\}$, where $\boldsymbol{\beta}$ is a vector of parameters representing the strength of selection for $\mathbf{h}(\mathbf{x}, \mathbf{y})$, a vector of habitat covariates. Therefore, SSFs consider the step density as the product of resource selection $w(\mathbf{x}, \mathbf{y})$ and movement $\Phi(\mathbf{y}|\mathbf{x})$.

The ESF can be viewed as a special case of an SSF, where $w(\mathbf{x}, \mathbf{y})$ is based on two energetic covariates, and where $\Phi(\mathbf{y}|\mathbf{x})$ can be viewed as an “energy-independent” movement kernel, which is uniform over the whole study region (i.e. it cancels out in Equation 3). We consider $\Phi(\mathbf{y}|\mathbf{x})$ to be uniform based on the assumption that, in the absence of energetic constraints (i.e. a hypothetical animal that can move arbitrarily fast without expending energy), animals could travel anywhere in the study region. Here, selection against costs defines a movement model, as $C(\mathbf{x}, \mathbf{y})$ can account for aspects of animal movement that affect energy expenditure (e.g. speed and tortuosity). For a simple example, in the absence of selection for gains ($\beta_1 = 0$) and if the costs are proportional to the step length squared, the ESF reduces to a Gaussian random walk with variance inversely proportional to β_2 (Appendix A). Regardless of the exact cost formulation, the ESF eliminates the need to make any *a priori* assumptions about movement and availability, as they are captured by the selection against energetic costs. Similarly to iSSA (Avgar et al., 2016), this circumvents the notable difficulty of defining availability in habitat selection studies (Beyer et al., 2010), while assessing energetic processes.

The integrated approach of the ESF can also correct for bias in habitat selection parameters when an animal faces energetic trade-offs. For example, in a case where the acquisition of an energy-rich resource requires moving through high-resistivity habitat, ignoring the increased energetic costs may lead to underestimating the resource selection parameter. To address this issue, Eisaguirre et al. (2020) proposed modifying the movement kernel of an SSF to account more realistically for energetic costs. In contrast, the ESF offers an integrated solution where gains and costs are combined directly into the selection function.

2.3 Implementation

Consider a set of locations of an animal $\{\mathbf{x}_1, \mathbf{x}_2, \dots, \mathbf{x}_n\}$. The ESF defines the likelihood of the entire track as $L(\beta_1, \beta_2 \mid \mathbf{x}_1, \dots, \mathbf{x}_n) = \prod_{i=1}^{n-1} f(\mathbf{x}_{i+1} \mid \mathbf{x}_i)$, where $f(\mathbf{x}_{i+1} \mid \mathbf{x}_i)$ is the likelihood of a single step (Equation 1). However, it can be computationally demanding to calculate the exact likelihood, as this would require evaluation of w over the entire domain of integration Ω (i.e. continuously over the whole study region). In practice, we can approximate this likelihood using a case-control (i.e. use-availability) design (Forester et al., 2009; Thurfjell et al., 2014). Case-control designs contrast where the animal went (i.e. what they used) with where they could have gone (i.e. available habitat), and is common in habitat selection analyses. For each observed location \mathbf{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 $\{\mathbf{z}_{i1}, \mathbf{z}_{i2}, \dots, \mathbf{z}_{iK}\}$, we calculate the approximate likelihood as

$$\tilde{L}(\beta_1, \beta_2 \mid \mathbf{x}_1, \dots, \mathbf{x}_n) = \prod_{i=1}^{n-1} \frac{w(\mathbf{x}_i, \mathbf{x}_{i+1})}{\sum_{k=0}^K w(\mathbf{x}_i, \mathbf{z}_{ik})}, \quad (4)$$

where we define $\mathbf{z}_{i0} = \mathbf{x}_{i+1}$.

Ideally, we want to sample control locations $\{\mathbf{z}_{i1}, \mathbf{z}_{i2}, \dots, \mathbf{z}_{iK}\}$ from a uniform distribution across the whole habitat, Ω . However, this procedure can be computationally intense. To mitigate against this computational issue, we notice that the ESF (Equation 2) will typically be negligible when \mathbf{z}_{ij} is sufficiently far from the starting point of the step, \mathbf{x}_i . We therefore generate control locations over a sufficiently large neighbourhood of the start point (i.e. a disc of radius R) to obtain a good approximation of the likelihood (Appendix B). This sampling is not a model of movement or availability. Rather, we use control locations over a disc merely for computational convenience, whereas the availability can be viewed as arising from the effect of energetic costs on movement, $C(\mathbf{x}, \mathbf{y})$. Replacement of Ω by a disc of radius R can be viewed as a special case of importance sampling, to increase the precision of the Monte Carlo integration in 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 β_1, β_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 D, 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 S5).

2.4 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. Gains, G , and costs, C , need to be defined in units of energy (which could be standard units such as kJ or any other convenient unit), based on ecological and physical principles. Here, we focus on the energetic gains of foraging and costs of movement, but the approach can be extended if other environmental factors (e.g. temperature, weather) are important to energy gain or expenditure. In fact, we may not always be able to or even want to include all aspects of energetics, particularly when they are not important for inferences (e.g. when they are consistent between individuals and/or are not dependent on habitat). These covariates should be formulated carefully, as the inferences 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.

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 will 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. Furthermore, resources may be combined with movement data, in cases with strong empirical or hypothesized relationships between foraging potential and movement speed (Figure S4). Under this formulation, we can evaluate selection for foraging resources under a common energetic currency, rather than preference for individual resources.

Energetic costs will typically be formulated primarily in terms of movement (tortuosity and 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); 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; Shepard et al., 2013). Therefore, habitat features and movement data can be combined into a synthetic model of energy expenditure (see Section 3, Figure S4) or correlated to estimate the energetic

costs of control steps.

3 Case study

In this section, we present a case study of polar bears as an illustrative example of the ESF framework, in which we detail the process to define the energetic covariates and draw inferences. Polar bears are apex predators that forage on fat-rich prey (primarily seals) and inhabit highly dynamic sea ice environments. They have pronounced seasonal patterns of energy acquisition (i.e. hyperphagia in the spring followed by a hypopahgic period; Pilfold et al., 2012), as well as high energy expenditure associated with locomotion (Hurst et al., 1982a). Additionally, movement costs can be highly affected by the local sea ice conditions, such as ice concentration and drift speed (Durner et al., 2017; Griffen, 2018). Although these spatiotemporal interactions indicate that energetics may largely influence polar bear movement and space use, these mechanisms have yet to be analysed in a framework that considers selection of gains and costs. In this case study, we applied the ESF to solitary adult (> 5 years old) GPS-collared female polar bears in the Canadian Beaufort Sea. We used tracking data at a 4-hour resolution from the spring period of 2007-2011 (Figures 2; see Appendix E.1 for details of the study area, data acquisition, and data processing). We estimated 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 Energetic gains G

Polar bears forage primarily on ringed seals (*Pusa hispida*) and bearded seals (*Erignathus barbatus*), particularly during a hyperphagic period from mid-April to June (Pilfold et al., 2012). Therefore, we derived energetic gains from an RSF model of forage quality that covered our study (2007 – 2011) from Pilfold et al. (2014). This 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 the temporal and spatial extent of the original rasters, but not beyond the original range of habitat characteristics and season (Figure 2). For March – June of each year, 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. The resolution of the rasters was 6.25km and RSF values were zero in locations where sea ice was absent.

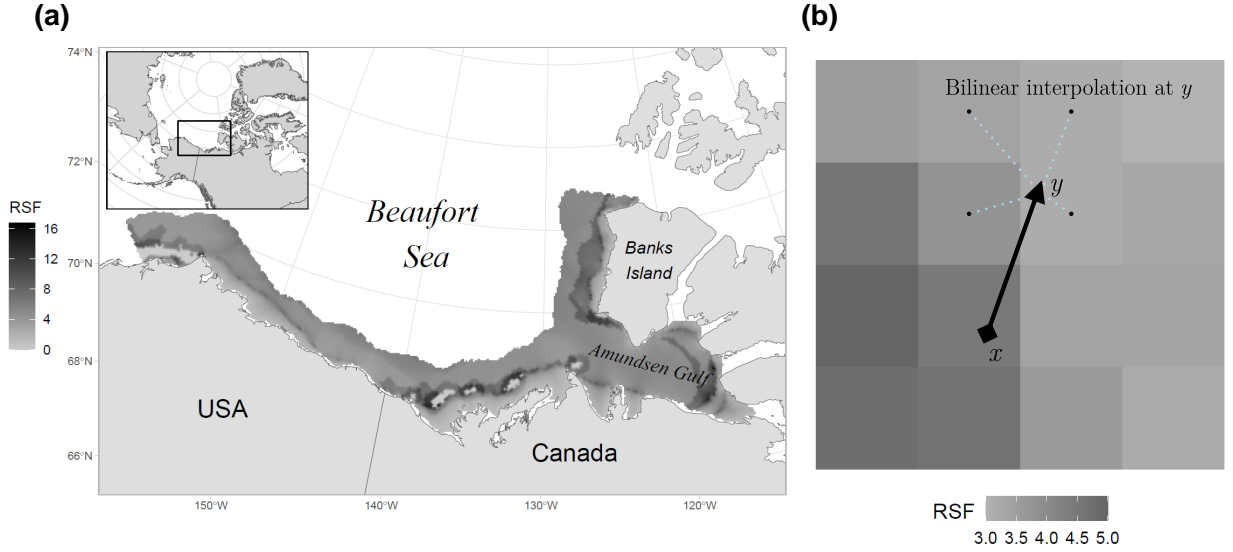


Figure 2: Illustration of energetic gains in polar bear case study. (a) Map of study area overlaid with an example seal biomass RSF (Pilfold et al., 2014). (b) Schematic representation of energetic gain evaluation for a step from x to y , using bilinear interpolation at y based on the four adjacent cells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

3.2 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. 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. 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* R 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. 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). These data included resting metabolic rates (i.e. basic maintenance costs) and accounted for the weight of the bear. 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* (Pya & Wood, 2015). 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).

3.3 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 B 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) and accounted for this in the ESF likelihood. 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*.

3.4 Results

We analysed 7,861 GPS locations from 23 GPS-collared adult female polar bears (locations per individual: 80 – 968). Energetic gains at each step (including controls) ranged from 0 to 27.9 (arbitrary units) and energetic costs ranged from 3.27 to 161 MJ. The median β_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 β_2 estimates showed a selection against costs, with a median of 0.57 (range 0.32, 0.97), and no CIs overlapped zero. We also compared the ESF to a null model (given as the simple random walk in Appendix A) and found that the ESF fit better than the null for all but three individuals (Appendix E.3).

3.5 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, suggesting that these might be

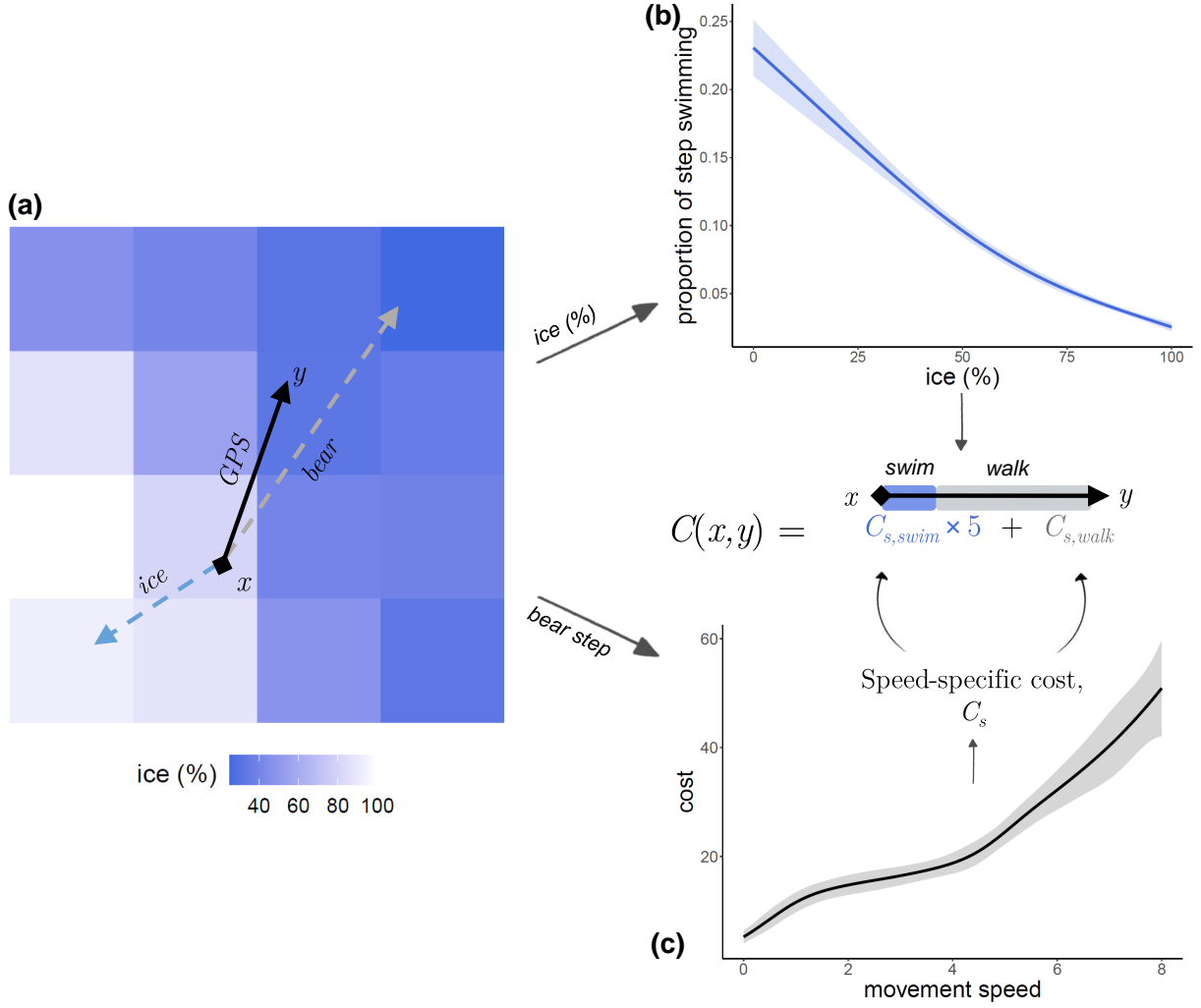


Figure 3: Schematic illustration of energetic cost evaluation in the polar bear case study, for an observed step starting at x and ending at y . (a) Arrows represent the observed movement step (black; GPS), ice drift (blue dashed; ice), and actual bear movement (grey dashed; calculated as GPS - ice). Ice concentration (%) is estimated at y with bilinear interpolation. (b) Modelled relationship between ice concentration and the proportion of the step spent swimming from Lone et al. (2018). 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. 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 $C_{s,walk}$.

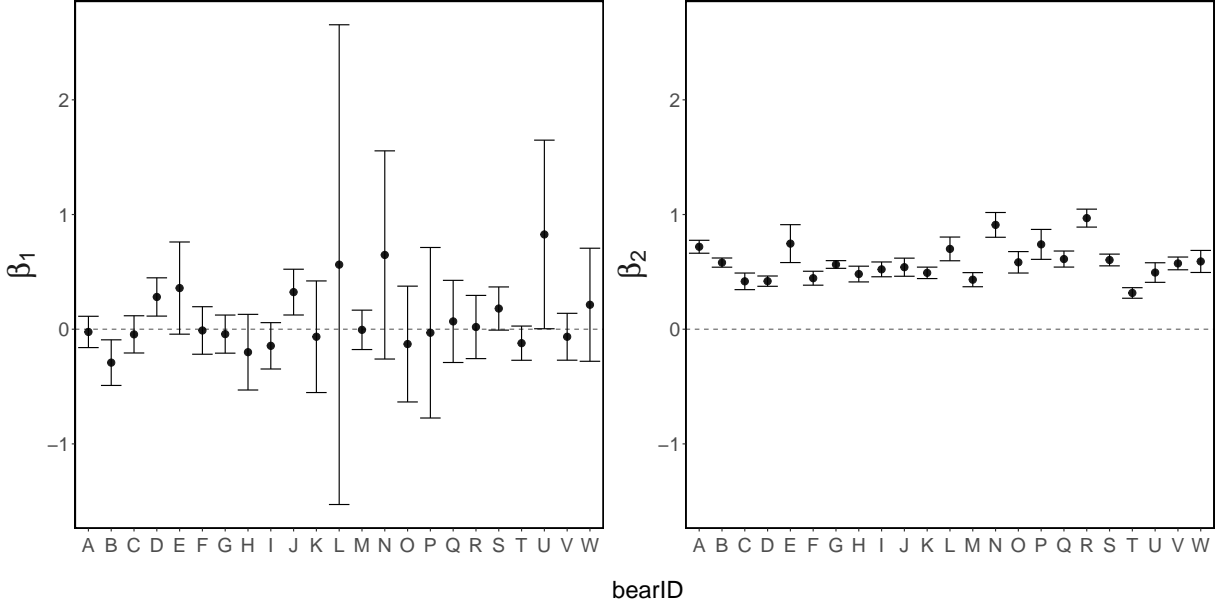


Figure 4: Estimated β_1 (selection for gains) and β_2 (selection against costs) coefficients of lone adult female polar bears ($N = 23$). Error bars are 95% CIs.

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). These mismatches could result in low variation between case and control locations, particularly if the tracking data is not at a biologically relevant resolution. Future studies could 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). For example, we defined gains from an RSF model, which is only an estimation of the true prey availability. However, accounting for covariate error is not standard in habitat selection studies, as methods remain analytically complex and uncertainty in environmental data is often unknown.

Our results suggest that most solitary female polar bears in the Beaufort Sea employed 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). 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 constant 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 (Galicía 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 could be tested in future research, which may require a more nuanced model formulation, while addressing annual, seasonal, demographic, and spatial variation in energy selection.

An alternative to the ESF would be an SSF with energetically-relevant covariates and a resource-independent movement kernel $\Phi(\mathbf{y}|\mathbf{x})$ derived from the polar bear tracking data. Energetic gains could be incorporated directly (i.e. as the seal RSF), but it is unclear how one would account for movement costs in that framework. One possibility may be to include ice concentration (or time swimming) as a covariate to capture the avoidance of energetically-costly open water areas. In that case, costs would be split between the movement kernel $\Phi(\mathbf{y}|\mathbf{x})$ (e.g. avoidance of long steps) and the weighting function $w(\mathbf{x}, \mathbf{y})$ (e.g. avoidance of open water), preventing the estimation of their combined effect. Therefore, the joint dependence of costs on speed and habitat (Figure 3) would be lost. Sea ice movement poses an additional challenge for applying a standard SSF, as a movement kernel based on the GPS tracks would include ice drift and not be a good description of the bears' movement. In the ESF, there is no need to specify a movement kernel prior to model fitting, and the effects of ice drift and ice concentration can be included directly in the energetic cost covariate.

4 Discussion

Evaluating the energetic basis of animal movement and habitat selection remains a topical issue in ecology (Hooten et al., 2019; Eisaguirre 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. Eisaguirre et al. (2020) also used an energetic approach to incorporate costs into the SSF availability kernel to ascertain

the selection for resources once such costs had been accounted for. However, the ESF explicitly accounts for gains and costs in the selection process, thereby considering energetic mechanisms to be the goal of inference. We consider our model an important step in understanding the contribution of energy in observed space use patterns.

Inherently, step selection analyses are sensitive to the spatial and temporal scale of the telemetry and covariate data (Munden et al., 2021). In the ESF, the spatial scale of the energetic covariates needs to 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 selection of intervals between telemetry locations and continuous-time analogues of SSFs may prove useful to overcome these scale dependencies. High frequency data (e.g. once per second) can also overcome this, as one can infer the turning points the animals make and then look at the selection for each turn (Munden et al., 2021). 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).

In the SSF framework, an alternative to using the ESF would be to use a standard movement kernel $\Phi(\mathbf{y}|\mathbf{x})$ (e.g. based on empirical distributions of step lengths and turning angles; Fortin et al., 2005), and include covariates that have energetic importance in the weighting function $w(\mathbf{x}, \mathbf{y})$. This formulation would separate the energetic contributions of the movement and habitat, which the ESF combines through a common currency to facilitate energy-based inferences. As illustrated in Section 3, the energetic covariates can be linked to movement and habitat through complex non-linear relationships, which would be difficult to include in an SSF. An integrated energetic approach may be particularly important for species that inhabit a moving environment. In this case, $\Phi(\mathbf{y}|\mathbf{x})$ is not an inaccurate depiction of voluntary movement or energy expenditure, but the effect of a mobile substrate can easily be incorporated into $C(\mathbf{x}, \mathbf{y})$. Lastly, since the ESF is a movement-based model, its inferences differ from previous work linking energetics to RSFs that cannot directly incorporate the costs of locomotion (e.g. Long et al., 2014).

The ESF has great potential for methodological extensions, due to its close theoretical and practical links to existing methods (SSFs and iSSA). For example, we could 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). It may also be possible to incorporate energetic state (i.e. level of satiation) to better reflect the physiological demands and constraints of gaining energy (i.e. recharge dynamics; Hooten et al., 2019). Ultimately, the ESF is a widely applicable and flexible method to combine energy, movement, and habitat selection.

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Author contributions

JR Potts conceived the original idea for the model, with input from L Börger. NJ Klappstein and AE Derocher conceived and designed the polar bear application and energetics modelling. NJ Klappstein conducted the statistical analysis with assistance from T Michelot and input from all co-authors. NW Pilfold produced the seal RSF rasters and AE Derocher provided the polar bear telemetry data. NJ Klappstein wrote the manuscript with contributions from all co-authors.

Data accessibility

If the manuscript is accepted for publication, we will publish our data and accompanying code to Zenodo, where it will be archived with a permanent doi.

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