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Energy-based step selection analysis: modelling the energetic drivers of animal movement and habitat use

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Abstract

1. The energetic gains from foraging and costs of movement are expected to be key drivers of animal decision-making, as their balance is a large determinant of body condition and survival. 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.

2. To address this gap, we present a novel parameterisation of step selection functions (SSFs), that we term the energy selection function (ESF). In this model, the likelihood of an animal selecting a movement step depends directly on the corresponding energetic gains and costs, and we can therefore assess how moving animals choose habitat based on energetic considerations.

3. The ESF retains the mathematical convenience and practicality of other SSFs and can be quickly fitted using standard software. In this paper, we outline a workflow, from data-gathering to statistical analysis, and use a case study of polar bears (*Ursus maritimus*) to demonstrate application of the model.

4. We explain how defining gains and costs at the scale of the movement step allows us to include information about resource distribution, landscape resistance, and movement patterns. We further

demonstrate this process with a case study of polar bears, and show how the parameters can be interpreted in terms of selection for energetic gains and against energetic costs.

5. The ESF is a flexible framework that combines the energetic consequences of both movement and resource selection, thus incorporating a key mechanism into habitat selection analysis. Further, because it is based on familiar 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). In addition to other considerations (e.g., predator-avoidance), 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, models of animal movement often attempt to link space use to optimal foraging decisions, and to uncover the eco-evolutionary mechanisms behind observed spatial patterns.

Energy-based models are a tool to assess how animals make decisions based on movement costs and associated nutritional benefits. Despite long-standing interest in these fundamental mechanisms of space use, 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 when energy intake can be evaluated more realistically (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. In reality, the costs vary 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, and there are clear benefits to integrating them 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 (RSFs) 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

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(Schoener, 1971; Shepard et al., 2009; Cornioley et al., 2016). Although the idea of energy-based move-
ment 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. decision to move to food
patch), based on a latent process for the physiological state of an animal (e.g. its satiation or cumulative
energy balance). A simpler, yet effective, approach could be to extend step selection functions (SSFs; i.e.
movement-based habitat selection models) to answer similar questions in a widely used, flexible framework.

In this paper, we propose an energy-based SSF, that we refer to in short-hand as the energy selection
function (ESF). The ESF models the effect of energetic gains and costs on an animal's movement decisions,
therefore integrating movement and habitat selection in an energetic context. Mathematically, the ESF is
a special case of SSFs, and can be implemented using standard logistic regression software, facilitating its
uptake in applied studies. 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
further outline the workflow and interpretation through an illustrative case study of polar bears (*Ursus
maritimus*) in the Beaufort Sea, Canada.

2 Materials and Methods

2.1 The ESF

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

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

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 $\boldsymbol{y}$ (Forester et al., 2009; Potts et al., 2014), and with energy
preference modelled as,

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

In Equation 2, we refer to $w(\boldsymbol{x}, \boldsymbol{y})$ as the ESF, and $G(\boldsymbol{x}, \boldsymbol{y})$ and $C(\boldsymbol{x}, \boldsymbol{y})$ are the energetic gain and energetic
cost of the step, respectively (illustrated in Figure 1). In this form, β_1 quantifies the selection for energetic
gains $G(\boldsymbol{x}, \boldsymbol{y})$, formulated in terms of energetically beneficial resources, and β_2 is the strength of selection

59 *against* energetic costs $C(\boldsymbol{x}, \boldsymbol{y})$, formulated as habitat-specific movement costs (see Section 2.1.3 for guidance

60 on how to define covariates). The likelihood can be optimised with respect to β_1 and β_2, over all steps, to

61 estimate the set of parameters that maximise the likelihood of an animal selecting the observed locations

62 relative to the rest of the available habitat. The ESF can be viewed as a joint model of habitat selection

63 (captured as selection for energetic gain) and movement (with selection against energetic costs).

64   When estimated together, the ESF parameters can provide support for different energy maximization

65 strategies in optimal foraging theory: an increase in β_1 represents stronger selection for gains (i.e. stronger

66 intake-maximization; Figure 1, scenario 1) and an increase in β_2 represents stronger selection against en-

67 ergetic costs (i.e. stronger cost-minimization; Figure 1, scenario 2). Either of these outcomes represent

68 strategies to maximize net energetic balance, and the ESF can assess whether animal movement is driven by

69 gains, costs, or both. If $G(\boldsymbol{x}, \boldsymbol{y})$ and $C(\boldsymbol{x}, \boldsymbol{y})$ are in the same units, then β_1 and β_2 can be directly compared

70 within the same model. However, even if the units are unknown, the ESF may still be used to compare

71 how strategies vary between individuals, time periods (e.g. seasons), demographic groups (e.g. juveniles vs.

72 adults), or any other ecologically-important grouping.

2.1.1   Comparison to other habitat selection models

74 The ESF uses the same basic modelling approaches as SSFs. Both models are used to analyse autocorrelated

75 animal tracking data and describe habitat selection at the scale of the observed movement step. SSFs consider

76 that movement constraints limit the habitat availability, and give the likelihood of a movement step ending

77 at location $\boldsymbol{y}$ given that it started at location $\boldsymbol{x}$ in the study region Ω as

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

79 The first term, $\Phi(\boldsymbol{y}|\boldsymbol{x})$, is the resource-independent movement kernel, which describes how an animal would

80 move in a homogeneous landscape or in the absence of resource preference (Forester et al., 2009). The second

81 term, $w(\boldsymbol{x}, \boldsymbol{y})$, is a weighting function and represents resource selection without movement constraints. The

82 weighting function is typically defined as: $w(\boldsymbol{x}, \boldsymbol{y}) = \exp\{\boldsymbol{\beta} \cdot \boldsymbol{h}(\boldsymbol{x}, \boldsymbol{y})\}$, where $\boldsymbol{\beta}$ is a vector of parameters

83 representing the strength of selection for $\boldsymbol{h}(\boldsymbol{x}, \boldsymbol{y})$, a vector of habitat covariates. Therefore, the step density

84 of an SSF model is the product of resource selection $w(\boldsymbol{x}, \boldsymbol{y})$ and movement $\Phi(\boldsymbol{y}|\boldsymbol{x})$.

85   The ESF can be viewed as a special case of an SSF, where $w(\boldsymbol{x}, \boldsymbol{y})$ is based on two energetic covariates, and

86 where $\Phi(\boldsymbol{y}|\boldsymbol{x})$ can be viewed as an "energy-independent" movement kernel, which is uniform over the whole

87 study region (i.e. it cancels out in Equation 3). We consider $\Phi(\boldsymbol{y}|\boldsymbol{x})$ to be uniform based on the assumption
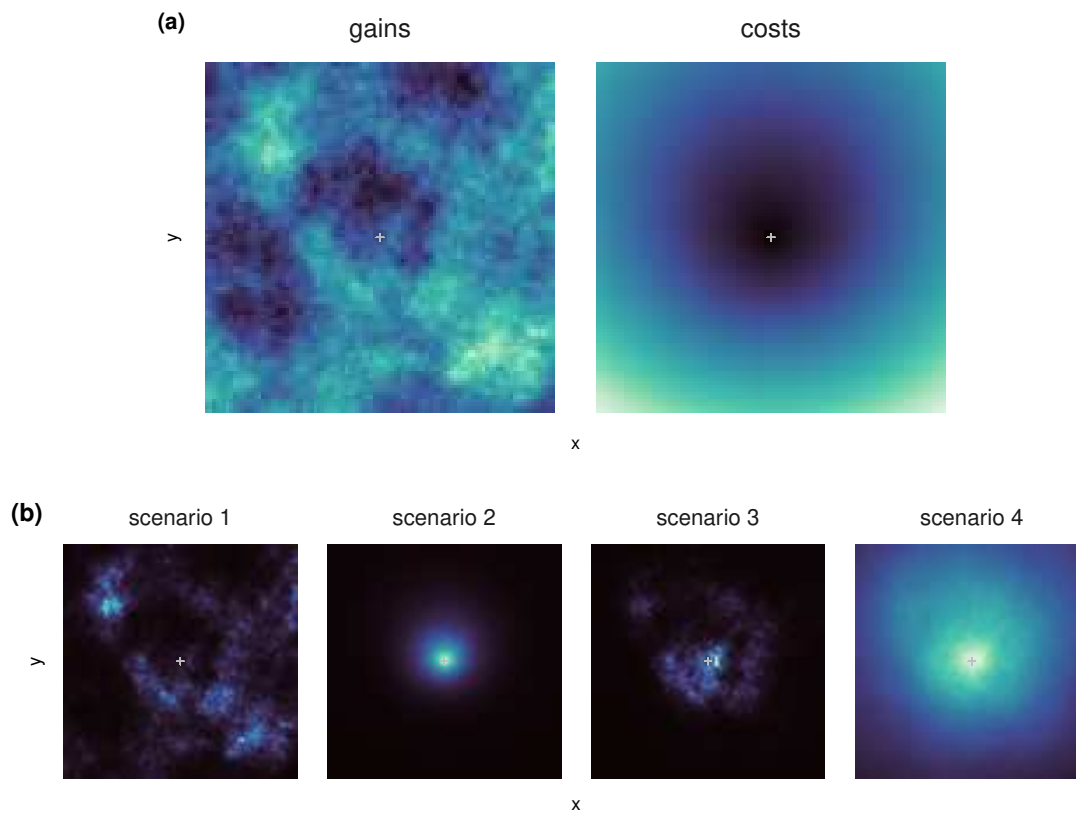
Figure 1: (a) Simulated rasters of energetic gains and energetic costs, and (b) corresponding ESFs. In (a), energetic gains were simulated as a random covariate field and energetic costs were defined as a product of the step length and turning angle from the central location (+), assuming that the animal was facing up the y-axis before turning. In (b), the ESF was calculated as $ESF = \exp(\beta_1 \times gains - \beta_2 \times costs)$ with different values of β_1 and β_2 to represent different movement scenarios: scenario 1 represents movement driven primarily by gain-maximisation (high β_1, low β_2), scenario 2 represents movement driven primarily by cost-minimisation (high β_2, low β_2), scenario 3 represents movement driven strongly by both gains and costs (high β_1, high β_2), and scenario 4 represents a low effect of both (low β_1, low β_2). In all panels, lighter colours represent higher values.

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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 $C(\boldsymbol{x}, \boldsymbol{y})$ 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 the assumption that availability is known, as this is captured by the selection against energetic costs. Therefore, similar to integrated step selection analysis (iSSA; Avgar et al., 2016), the ESF circumvents the difficulty of defining availability in habitat selection studies (Beyer et al., 2010), while simultaneously assessing energetic processes. For this reason, it stands in contrast with the approach of Latombe et al. (2014), where the ratio of gains over costs was included as a covariate in an SSF with a non-uniform function Φ (based on empirical distributions of step lengths and turning angles). That model measures the effects of gains and costs once movement constraints have been accounted for, rather than integrate all aspects of movement and habitat selection into energetic variables.

2.1.2 Implementation

Consider a set of locations of an animal $\{\boldsymbol{x}_1, \boldsymbol{x}_2, \ldots, \boldsymbol{x}_n\}$. The ESF defines the likelihood of the entire track as $L(\beta_1, \beta_2 \mid \boldsymbol{x}_1, \ldots, \boldsymbol{x}_n) = \prod_{i=1}^{n-1} f(\boldsymbol{x}_{i+1}|\boldsymbol{x}_i)$, where $f(\boldsymbol{x}_{i+1}|\boldsymbol{x}_i)$ is the likelihood of a single step (Equation 1). In many cases, the exact likelihood is computationally intractable, as it includes the integral of w over the study region Ω. 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 habitat characteristics at locations where the animal went (i.e. what it used) with where it could have gone (i.e. available habitat), and they are common in habitat selection analyses. For each observed location $\boldsymbol{x}_i$ (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 $\{\boldsymbol{z}_{i1}, \boldsymbol{z}_{i2}, \ldots, \boldsymbol{z}_{iK}\}$, we calculate the approximate likelihood as

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

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

This numerical integration requires sampling control locations $\{\boldsymbol{z}_{i1}, \boldsymbol{z}_{i2}, \ldots, \boldsymbol{z}_{iK}\}$ from a uniform distribution across the whole habitat, Ω, which can be computationally intensive if Ω is large. To reduce the

117 computational cost, we notice that the ESF (Equation 2) will typically be negligible when $\boldsymbol{z}_{ij}$ is sufficiently

118 far from the starting point of the step, $\boldsymbol{x}_i$ (i.e. as costs get very large). We therefore generate control lo-

119 cations over a sufficiently large neighbourhood of the start point (i.e. a disc of radius R) to obtain a good

120 approximation of the likelihood (Appendix B). In most cases, it may be sufficient to choose R to be slightly

121 larger than the animal's longest observed step, based on the assumption that the likelihood of a step longer

122 than this is negligible (see Appendix B for evaluation of R size). This sampling is not a model of movement

123 or availability (e.g. as in Arthur et al., 1996). Rather, we use control locations over a disc for computational

124 convenience, and the availability can be viewed as arising from the effect of energetic costs on movement,

125 $C(\boldsymbol{x}, \boldsymbol{y})$. Replacing Ω by a disc of radius R can be viewed as a special case of importance sampling, to

126 increase the precision of the Monte Carlo integration in Equation 4.

127   Given that the ESF uses the same general formulation and case-control design as SSFs, model fitting can

128 be done using the same statistical techniques and software. We can estimate β_1, β_2 with maximum likelihood

129 estimation (MLE), with regards to Equation 4, using numerical optimizers (e.g. *optim* in R) or software for

130 conditional logistic regression (e.g. the R function *clogit*, package *survival*). Therefore, implementation is

131 fast and based on techniques that many practitioners may be familiar with. In Appendix D, we verify these

132 implementation methods with a technical simulation, which showed accurate inferences under different levels

133 of spatial autocorrelation and number of control locations used (Figure S5).

2.1.3   Defining the energetic covariates

135 The ESF is applicable to any system where there is adequate energetic data, and the covariates must be

136 formulated specifically to each study. Gains, G, and costs, C, need to be defined in units of energy (which

137 could be standard units such as kJ or any other convenient unit), based on ecological and physical principles.

138 Here, we focus on the energetic gains of foraging and costs of movement, but the approach can be extended

139 if other environmental factors (e.g. temperature, weather) are important to energy gain or expenditure. In

140 fact, we may not always be able to or even want to include all aspects of energetics, particularly when

141 they are not important for inferences (e.g. when they are consistent between individuals and/or are not

142 dependent on habitat). These covariates should be formulated carefully, as the inferences from the ESF

143 necessarily depend on the quality of the estimated energetic variables. Definitions of G and C rely on

144 carefully evaluating complex interactions between movement and habitat, and mischaracterization may lead

145 to parameter estimates that do not truly represent energy selection.

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

147 can be derived from environmental data (e.g. NDVI, prey or vegetation biomass; Fortin et al., 2003; Pilfold

148 et al., 2014). Many recent studies have presented methods to derive energy intake of herbivores at the

149 scale of a movement step based on vegetation biomass (Latombe et al., 2014; Merkle et al., 2014; Brooke

150 et al., 2020; Duparc et al., 2020). Metrics will contain relevant information to represent consumable and

151 digestible biomass, and more than one resource can be incorporated into G if they are weighted based on

152 their energetic contribution. Furthermore, resources may be combined with movement data, in cases with

153 strong empirical or hypothesized relationships between foraging potential and movement speed (Figure S4).

154 Under this formulation, we can evaluate selection for foraging resources under a common energetic currency,

155 rather than preference for individual resources.

156 Energetic costs will typically be formulated primarily in terms of movement (tortuosity and speed; Taylor

157 et al., 1970; Wilson et al., 2013), which can be quantified from geographical positioning system (GPS)

158 location data. To inform the costs of movement steps, GPS metrics can be combined with captive studies

159 (e.g. treadmills; Bidder et al., 2017) and field measures that more directly measure energy expenditure

160 and behaviour (e.g. doubly-labelled water, heart rate, dynamic body acceleration; Pagano & Williams, 2019;

161 Wilson et al., 2020). The cost of movement is also affected by habitat factors, such as substrate penetrability

162 (soft vs. hard; Crête & Larivière, 2003), slope (Halsey, 2016), and resistivity (e.g. wind and water currents;

163 Shepard et al., 2013). Therefore, habitat features and movement data can be combined into a synthetic

164 model of energy expenditure (see Section 2.2, Figure S4) or correlated to field measures to estimate the

165 energetic costs of control steps.

2.2 Case study

167 In this section, we present a case study of polar bears as an example of the ESF framework, in which we detail

168 the process to define the energetic covariates and draw inferences. Polar bears are apex predators that forage

169 on fat-rich prey (primarily seals) and inhabit highly dynamic sea ice environments. They have pronounced

170 seasonal patterns of energy acquisition (i.e. hyperphagia in the spring followed by a hypophagic period;

171 Pilfold et al., 2012), as well as high energy expenditure associated with locomotion (Hurst et al., 1982a).

172 Additionally, movement costs can be highly affected by the local sea ice conditions, such as ice concentration

173 and drift speed (Durner et al., 2017; Griffen, 2018). Although these spatiotemporal interactions indicate

174 that energetics may largely influence polar bear movement and space use, these mechanisms have yet to

175 be analysed in a framework that considers selection of gains and costs. In our case study, we applied

176 the ESF to solitary adult (> 5 years old) GPS-collared female polar bears in the Canadian Beaufort Sea.

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177 We used tracking data at a 4-hour resolution from the spring (March - June) of 2007-2011 (Figure 2; see

178 Appendix E.1 for details of the study area, data acquisition, and data processing). All field research was

179 conducted under Government of Northwest Territories Department of Environment and Natural Resources

180 permits (WL003322, WL005372, WL005596, WL007376) and animal handling procedures were approved

181 by the University of Alberta BioSciences Animal Care and Use Committee. We estimated energetic gains

182 from an energetically-weighted RSF of seal kills, and develop a cost model for use with GPS telemetry data.

183 Therefore, we consider polar bear energetics at the scale of movement-based habitat selection.

2.2.1 Energetic gains G

185 Polar bears forage primarily on ringed seals (*Pusa hispida*) and bearded seals (*Erignathus barbatus*), par-

186 ticularly during a hyperphagic period from mid-April to June (Pilfold et al., 2012). Therefore, we derived

187 energetic gains from an RSF model of forage quality that covered our study (2007 – 2011) from Pilfold et al.

188 (2014). This RSF modelled locations of seals killed by polar bears, weighted by biomass, relative to habitat

189 characteristics. The most important habitat covariates in the weighted RSF model were distance from land,

190 bathymetry, distance from shorefast ice boundary, regional sea ice concentration, floe edge, and ice type (for

191 details, see Pilfold et al., 2014). Because the RSF incorporated both seal kill biomass and abundance, we

192 assumed the RSF value to be proportional to energetic return. We extended the temporal and spatial extent

193 of the original rasters, but not beyond the original range of habitat characteristics and season (Figure 2),

194 and we created daily rasters which encompassed approximately 100km off-shore along the coast of Alaska

195 and Canada (from approximately 160°W to 115°W), including the Amundsen Gulf and regions adjacent to

196 Banks Island. The resolution of the rasters was 6.25km and RSF values were zero in locations where sea ice

197 was absent.

2.2.2 Energetic costs C

199 We formulated costs based on the movement costs of captive polar bears, combined with environmental

200 covariates to represent field conditions (Figure 3). Telemetry locations arise from a combination of active

201 bear movement and passive displacement caused by ice drift. Therefore, we defined a step as the active

202 bear movement between telemetry locations, corrected for ice drift following Klappstein et al. (2020), using

203 drift data from the National Snow and Ice Data Center (Polar Pathfinder Daily 25km EASE-Grid Sea Ice

204 Motion Vectors; Tschudi et al., 2019). In the following, we used the GPS locations to evaluate environmental

205 variables, whereas we used the tracks corrected for ice drift to measure movement speed. At each step, a
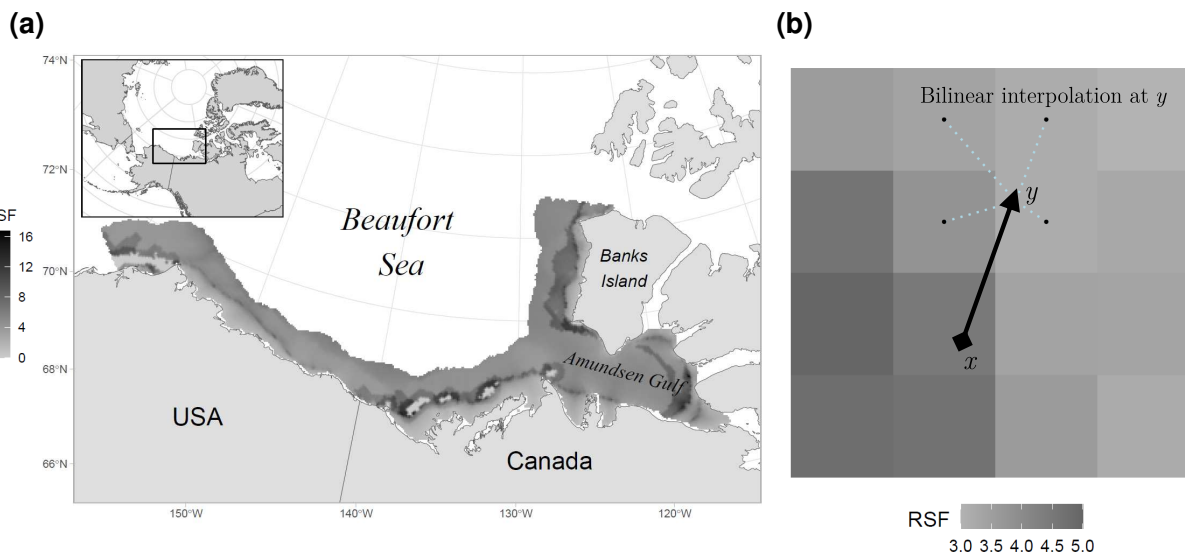
Figure 2: Illustration of energetic gains in polar bear case study. (a) Map of study area overlaid with an example of the seal biomass RSF. (b) Schematic representation of energetic gain evaluation for a step from $\boldsymbol{x}$ to $\boldsymbol{y}$, using bilinear interpolation at $\boldsymbol{y}$ based on the four adjacent cells (black dots).

bear can either be swimming or walking on sea ice, which have different energetic costs (e.g. Griffen, 2018; Pagano et al., 2018). Using spring/summer (March - August) 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). This model does not have an intercept at 1, as expected, suggesting that time spent in water may be underestimated for low ice concentration (Figure 3b). This can be partially be explained by the tendency of satellites to underestimate ice concentration (e.g., Castro de la Guardia et al. 2017 found that bears were still on ice when satellite imagery indicated ice concentration of 0%). Although underestimation of time spent in water could result in conservative cost estimates, it is the best data available. Using this GAM, we estimated proportion of time spent in water for each polar bear step, based on its interpolated ice concentration value (AMSR-E 3.125 km grid Version 5.4; Spreen et al., 2008), and assumed the proportion of time in water 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 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; Pagano & Williams, 2019).

As suggested in Section 2.1.3, movement tortuosity (i.e. turning angle) may also affect the costs of movement, and this effect could be included in analyses of high-resolution movement data (Wilson et al., 2013). Although small-scale tortuosity might not appear at a 4-hour resolution, directional persistence may be in place even at this coarser scale, due to large-scale targets of attraction (e.g. foraging patches, mating sites), environmental features (e.g., the floe edge), or behaviours (e.g. migration, site fidelity), on which we do not have sufficient information. In principle, if the energetic return of large-scale processes was known, it could be captured using a multi-scale ESF similar to the approach of Bastille-Rousseau et al. (2018). Instead, in Appendix F, we show how turning angle can be incorporated as a separate term in the ESF (similar to Avgar et al., 2016; Brooke et al., 2020) that encapsulates in a single energy-agnostic term all the drivers of directional persistence about which we do not have information, and compare this to the ESF presented below.

2.2.3 Fitting the ESF

We eliminated locations that were outside the spatiotemporal extent of the seal raster (Figure 2), which removed 34.1% of all locations (Figure 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 and Appendix D for number of controls). 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 fitted the ESF with the *clogit* function (from the R package *survival*) separately for each individual bear. Following Forester et al. (2009), we calculated robust standard errors to account for residual autocorrelation, which can lead to the underestimation of variance (details in Appendix G). We used Monte Carlo cross-validation to investigate the predictive performance of the model (as described by Fortin et al., 2009, full details in Appendix H). The general idea of cross-validation is to repeatedly fit the model to a random subset of the data (training data set), and check how frequently it correctly distinguishes between the observed steps and control steps in the remaining data (validation data set). The output of each iteration of this procedure is a Spearman rank
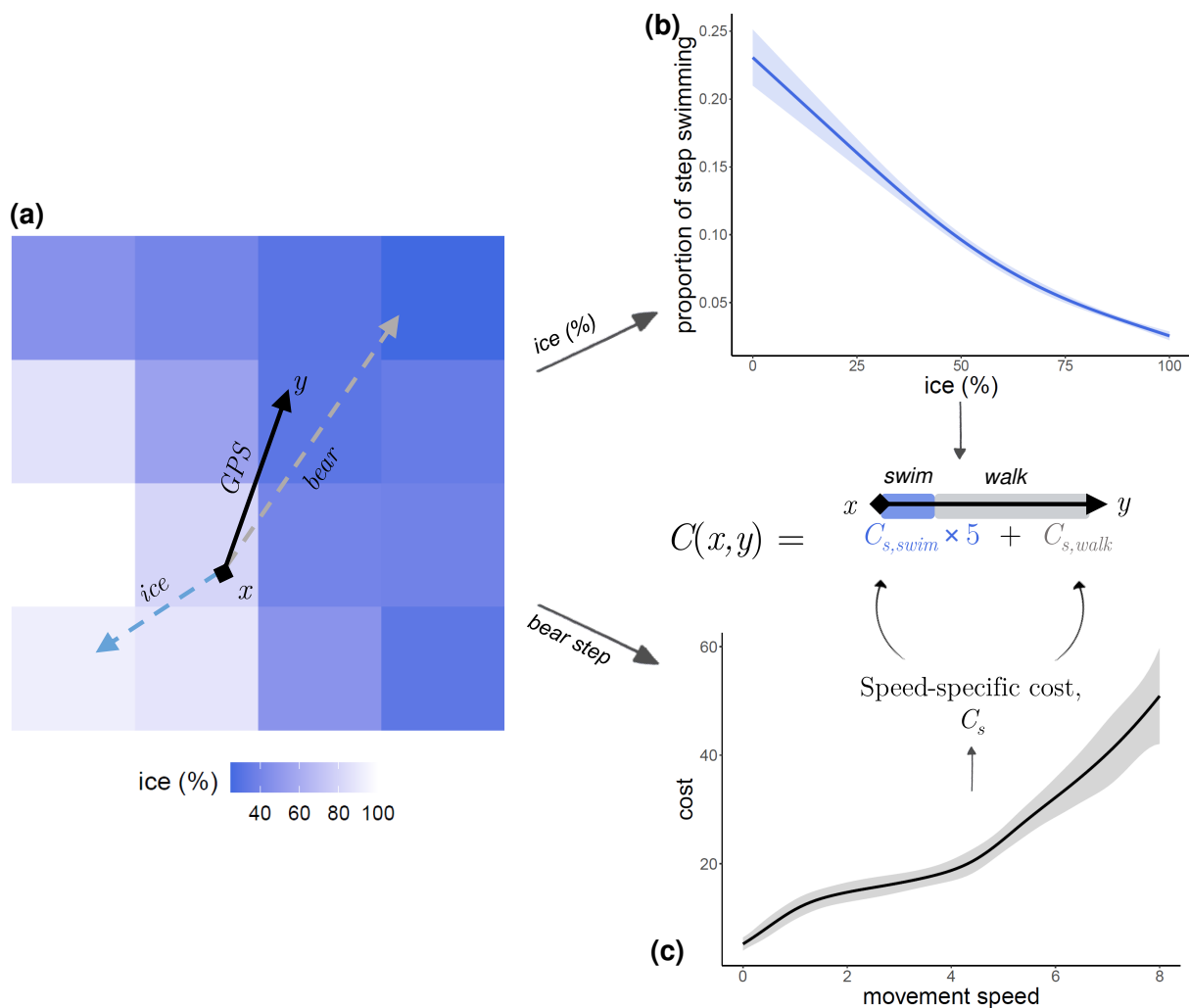
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Figure 3: Schematic illustration of energetic cost evaluation in the polar bear case study, for an observed step starting at $\boldsymbol{x}$ and ending at $\boldsymbol{y}$. (a) Arrows represent the observed movement step (black; GPS), ice drift (blue dashed; ice), and actual bear movement (grey dashed; calculated as GPS - ice). Ice concentration (%) is estimated at $\boldsymbol{y}$ with bilinear interpolation (illustrated in Figure 2b). (b) Modelled relationship between ice concentration (ice %) and the proportion of the step spent swimming based on 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 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 $C(\boldsymbol{x}, \boldsymbol{y})$ is the sum of $C_{s,swim}$ multiplied by 5 (to represent the higher costs of swimming) and $C_{s,walk}$.

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correlation coefficient, $-1 \leq r_s \leq 1$, which measures how consistently the case locations of the validation data set are ranked higher than the corresponding control locations. If the model has high predictive power, then the rank of the case locations is high and this is reflected in a high Spearman rank correlation coefficient, i.e., close to 1 . For comparison, we also repeated this procedure on the control locations only (i.e., without the case) to assess how often a random location would be chosen by chance alone.

2.2.4 Comparison to an SSF

To illustrate how an SSF based on environmental features differs from the ESF, we fitted an SSF model (given by Equation 3), with non-energetic covariates and a resource-independent movement kernel $\Phi(\boldsymbol{y}|\boldsymbol{x})$ derived from the polar bear tracking data. We included environmental covariates that contribute to G and C, but in a non-energetic form that are more typical in polar bear habitat selection analyses (e.g., McCall et al., 2016; Johnson & Derocher, 2020). Ice concentration is an important covariate for two reasons: i) it is a central component of C (i.e. it determines the proportion of time swimming; Lone et al., 2018), and ii) it is an important predictor in the seal RSF of G (i.e. there is a quadratic effect of ice concentration, which predicts highest biomass at approximately 85%; Pilfold et al., 2014). Therefore, we included both a linear and quadratic effect of ice concentration (ice and ice^2). We also included ocean depth ($depth$), interpolated from the International Bathymetric Chart of the Arctic Ocean (Version 4; Jakobsson et al., 2020), which contributes to energetic gains (i.e. greater seal kill biomass at greater depths; Pilfold et al., 2014). Lastly, we included sea ice drift speed ($drift$) as a covariate, as it affects the costs of moving any given geographic distance (Durner et al., 2017; Klappstein et al., 2020). We fitted the SSF using the same implementation techniques as the ESF, but generated controls based on the observed movement of the polar bears: we fitted a gamma distribution to step lengths and a wrapped Cauchy distribution to turning angles, and used these to randomly sample 20 control locations for each observed (case) location (as in Forester et al., 2009). We fitted and tested the predictive power of an SSF with cross-validation for each individual, following the same procedures described in Section 2.2.3.

3 Results

3.1 ESF results

We analysed $7,526$ GPS steps from 23 GPS-collared adult female polar bears (steps per individual: $78-946$). Among case steps, the median energetic gain was 4.4 (range: $0-20.3$; arbitrary units, assumed to be

proportional to energy), while controls had a median energetic gain of 4.3 (range: $0 - 28.1$). The median energetic cost of case steps was 8.1 MJ (range: $3.3 - 44.1$ MJ) and control steps had a median cost of 19.7 MJ (range: $3.6 - 124$ MJ). The median β_1 estimate was 0.10 (range $-0.32, 0.96$), with three estimates with 95% CIs that did not overlap zero (Figure 4). Of these, two bears appeared to select for energetic gains ($\beta_1 \pm \text{SE} = 0.42 \pm 0.14$; 0.40 ± 0.17) and one bear appeared to select against energetic gains ($\beta_1 \pm \text{SE} = -0.32 \pm 0.16$). Conversely, all β_2 estimates showed a selection against costs, with a median of 0.57 (range $0.27, 0.96$), and no CIs overlapped zero. For every individual, cross-validation indicated that the ESF better predicted polar bear movement than what would be expected by chance (i.e. mean individual r_s was always larger for the observed than random). Across all individuals, mean r_s (range) was 0.56 (0.20, 0.89) for observed and -0.009 (-0.68, 0.77) for random. Further, we performed cross-validation on both a gain-only and a cost-only model, which showed generally low predictive power of energetic gains and higher predictive power of energetic costs (Appendix H.1).
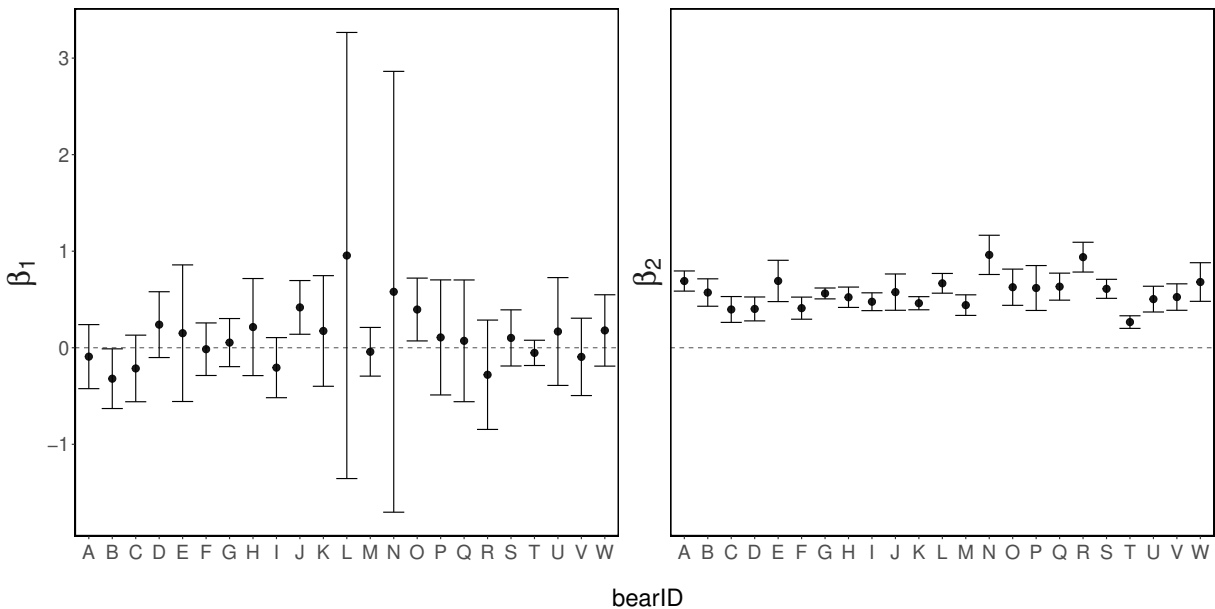

Figure 4: Estimated β_1 (selection for gains) and β_2 (selection against costs) coefficients of lone adult female polar bears ($n = 23$). Error bars are robust 95% CIs.

3.2 SSF results

Of the 23 individual bears, 8 had a statistically clear linear effect of ice concentration (i.e., robust 95% CIs for β_{ice} did not overlap 0), 7 of which also showed evidence of a quadratic effect (i.e., ice^2). For these 7

295 bears, estimates of β_{ice} were all positive (median: 8.05, range: 4.80 to 15.0), and estimates of β_{ice^2} were all

296 negative (median: -5.59, range: -8.83 to -1.39). These results indicate that some bears select for an optimal

297 range of ice concentration, which we estimated to range from 61% to 100%. Ocean depth was only found

298 to be an important predictor for 2 bears, 1 with a clear positive effect (i.e. selection for shallower regions;

299 $\beta_{depth} \pm SE = 3.08 \pm 0.99$) and 1 with a clear negative effect ($\beta_{depth} = -20.3 \pm 9.70$). Ice drift only had a clear

300 negative effect for 1 bear ($\beta_{drift} = -3.95 \pm 1.62$), and all other estimates had robust CIs that overlapped

301 0. Here, we only presented the ranges of estimates (across individuals) with statistically clear effects, but

302 full results including uncertainty are in Figure S11 of the supplementary material. Cross-validation scores

303 indicated that the SSF did not better predict polar bear movement better than would be explained by

304 random chance alone: individual mean Spearman rank correlation coefficients (r_s) of case locations had a

305 mean of 0.03 (range: -0.71 to 0.70), whereas the controls (proxy for random) had a mean of -0.07 (range:

306 -0.79 to 0.59). Note, these cross-validation results cannot directly be compared to those of the ESF, due to

307 differences in null models (i.e. distribution of control locations), but see Appendix I for an AIC-based model

308 comparison.

4 Discussion

310 Our proposed method to estimate the energy preferences of animals is similar to recent approaches to

311 combine movement and habitat (Avgar et al., 2016; Michelot et al., 2019), but the ESF uniquely integrates

312 both factors into energetic covariates. Therefore, the ESF adopts a purely energetic perspective, moving

313 away from habitat selection analyses that focus on environmental attributes. In this discussion, we start

314 with an interpretation and contextualisation the results of the polar bear case study, followed by a more

315 general discussion of the ESF method.

4.1 Discussion of the polar bear case study

317 In the case study, we found a strong pattern of selection against energetic costs in all individuals, but only

318 three showed evidence of selection for ($n = 2$) or against ($n = 1$) energetic gains. There was large uncertainty

319 in β_1 for most bears. One possible factor is that, if the values of gains for case and control locations did

320 not cover a wide enough range, it would provide little information about the effect. This can happen when

321 spatial autocorrelation in the covariate is high, or if the raster grid cells are large compared to observed steps,

322 such that most steps do not overlap multiple cells (Boyce et al., 2003; Boyce, 2006; Northrup et al., 2013).

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323 As both gains and costs incorporate ice concentration, we assessed the collinearity between the energetic
324 covariates. Although we only found a low to moderate correlation (Pearson correlation $= -0.3$), this might
325 have inflated the uncertainty of the parameter estimates. Further, the energetic covariates were imperfect
326 representations of intake and expenditure; we defined gains from an RSF model, which is only an estimation
327 of the true prey availability (Pilfold et al., 2014), and cost estimates were also model-based. The error in
328 these covariates could lead to either an underestimation of effects (e.g. if bears do select for seals, but the
329 gains do not accurately represent this), or overestimation of effects, as we did not propagate this covariate
330 error when estimating uncertainty. In studies where the energetic gains can be more directly measured (e.g.
331 ungulates and vegetation biomass; Brooke et al., 2020), we expect that the corresponding selection parameter
332 may be estimated more precisely, leading to more detailed insights into movement strategies of animals.

333 Our results suggest that movement of the solitary female polar bears in our study was driven by reducing
334 energy expenditure (i.e. cost-minimisation), but we found little evidence of an effect of energetic gains (i.e.
335 gain-maximisation). Cost-minimisation could arise due to high predictability of energetic costs, based on
336 internal factors and mechanical movement constraints, while intake-maximisation would require polar bears
337 to have knowledge of the unpredictable seal distribution (Ramsay & Stirling, 1986). At the landscape level,
338 polar bear distribution correlates positively to seal kill biomass (Pilfold et al., 2014), but we did not observe
339 this at the scale of the movement step, which may be reflective of local variability in the probability of
340 killing a seal. This is similar to the general observation of Fryxell (1997) that "sloppy foragers" (i.e., animals
341 whose movement is primarily determined by cost-minimisation rather than gain-maximisation) tend to do
342 well in situations where the distribution of energetic gains is unpredictable. Although all estimates of β_2
343 were positive, there was some inter-individual variability: for an increase in costs of 1MJ (with fixed gains),
344 the likelihood of taking a step decreased by 24% (i.e., lowest β_2) to 62% (i.e., highest β_2). This variability in
345 selection against costs reveals differences in movement behaviour, suggesting that some bears are more averse
346 to the energetic risk of costly steps. The absence of a statistically clear effect of energetic gains could also
347 be due to temporal variation in foraging behaviour. Polar bears do not enter the main foraging period until
348 mid-April (Pilfold et al., 2012), solitary females forage less when sequestered into less favourable habitats
349 by courting males (for up to 18 days at a time; Stirling et al., 2016), and larger-scale drivers such as site
350 fidelity (Mauritzen et al., 2001) could also dominate movement patterns. However, we did not directly test
351 these hypotheses, which could be investigated in future research.

352 The energetic inferences are fundamentally different from those of the SSF, the latter of which measures
353 selection for environmental features separated from their energetic interpretation. Of the covariates included

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354 in the SSF, ice concentration had the most common effect and indicated that bears select for an optimal level

355 of ice cover. However, because ice concentration is detached from energetics, it is unclear to what extent this

356 effect is explained by avoidance of open water (i.e., costs) or selection of seal-rich areas (i.e., gains). Sea ice

357 movement poses an additional challenge for applying a standard SSF, as it is unclear whether the movement

358 kernel Φ should be based on the observed GPS steps or the drift-corrected steps. Both definitions of Φ

359 are flawed: the observed steps (our chosen approach) are poor descriptors of the bear's movement because

360 they include ice drift, and while the drift-corrected steps account for this problem, they cannot be tied to

361 spatial locations where the bear was. This standard SSF formulation separates drift from its contribution

362 to energetic costs, which depends on both speed and directionality, and we therefore lose information about

363 how bears move relative to ice.

4.2 General discussion and future directions

365 In our case study, we demonstrated how the ESF can be used in a system where movement and habitat

366 are related to energetics through complex interactions, and derived energetic costs based partially on the

367 effects of a moving environmental substrate. Animal movement in moving habitats is an under-explored area

368 of habitat selection modelling, for which the ESF provides an integrated solution. Without this integrated

369 approach, energetic contributions of movement and habitat are typically modelled separately. Therefore,

370 the ESF provides a parameterisation, with convenient implementation procedures, to obtain energy-based

371 inferences that are conceptually different from the environment-based inferences of SSFs. Since the ESF is

372 a movement-based model, its inferences differ from previous work linking energetics to RSFs that cannot

373 directly incorporate the costs of locomotion (e.g. Long et al., 2014). Eisaguirre et al. (2020) used a two-stage

374 energetic approach to incorporate costs into the SSF availability kernel to estimate the selection for resources

375 once such costs had been accounted for. Therefore, Eisaguirre et al. (2020) can account for bias in habitat

376 selection parameters when animals make energetic trade-offs; for example, in a case where the acquisition of

377 an energy-rich resource requires moving through a highly resistive habitat, ignoring the increased energetic

378 costs may lead to underestimating the resource selection parameter. The ESF can be used to achieve a

379 similar goal, but offers a one-stage integrated solution where gains and costs are combined directly into the

380 selection function. Therefore, in contrast to Eisaguirre et al. (2020), the ESF treats energetic mechanisms as

381 the goal of inference. The approach of Hooten et al. (2019) has a similar motivation of describing the effects

382 of physiological processes on animal movement. In their framework, the effects of environmental features on

383 energetic balance are estimated during model fitting, whereas we assume that they are known from data.

Their approach therefore allows for more detailed inferences into underlying physiological mechanisms, and may be more appropriate when the gains and costs cannot be evaluated *a priori*. The ESF offers an alternative to understand the contribution of energy to observed space use patterns in the standard framework of SSFs.

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 (e.g. this case study) or energy accumulation over a long period (e.g. in the case of kill sites) may not be apparent at the scale of finer 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, continuous-time analogues of SSFs, and high-frequency data may prove useful to overcome these scale dependencies. 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). For example, we could consider a state-switching ESF model, where an unobserved behavioural state determines the selection parameters for energetic gains and costs. A state-switching ESF model would allow us to assess behaviour-specific energy selection, and could be written as a hidden Markov model, similar to the state-switching SSF model of Nicosia et al. (2017). It may also be possible to incorporate temporal dynamics and energetic state (e.g. satiation or cumulative energy balance; Latombe et al., 2014) to better reflect the physiological demands and constraints of gaining energy (i.e. recharge dynamics; Hooten et al., 2019). Further, it should be straightforward to include non-energetic terms (e.g., associated with predator risk) as interactions with gains and costs to assess how animals make energetic trade-offs with other aspects of survival. Here, we presented a re-imagining of SSFs, in which we use energy to summarise both habitat selection and movement. This approach is widely applicable, flexible enough to include a range of extensions, and can ultimately be used to build on foraging and movement theories from an energetic perspective.

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Conflicts of interests

We declare no conflict of interest.

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. All authors gave final approval for publication.

Data availability statement

Data and code from Zenodo https://doi.org/10.5281/zenodo.6319709 (Klappstein et al., 2022).

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