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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

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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

2 Understanding the mechanisms behind the spatial distributions of animals is a core consideration for animal
3 ecology (Kays et al., 2015). In addition to other considerations (e.g., predator-avoidance), space use patterns
4 are largely driven by the movement decisions made by animals whilst foraging. To increase their chances
5 of survival, animals should distribute themselves in space so as to maximize their access to energetically
6 rich resources, while minimizing the costs of travel (Pyke et al., 1977; Pyke, 2019). Consequently, models
7 of animal movement often attempt to link space use to optimal foraging decisions, and to uncover the
8 eco-evolutionary mechanisms behind observed spatial patterns.

9 Energy-based models are a tool to assess how animals make decisions based on movement costs and asso-
10 ciated nutritional benefits. Despite long-standing interest in these fundamental mechanisms of space use, it
11 remains a challenge to consider both energy expenditure and acquisition in a unified framework (Owen-Smith
12 et al., 2010, but see Hooten et al. 2019). Optimal foraging research often focuses on foraging benefits, using
13 approximate measures of forage quality or resource availability (e.g. Bastille-Rousseau et al., 2020), which
14 may not be proportional to energetic gains. Even when energy intake can be evaluated more realistically
15 (e.g. the energetic profitability of resources combined with biomass; Fortin et al., 2003), movement costs
16 are often ignored or assumed to increase linearly with time and/or distance. In reality, the costs vary de-
17 pending on factors such as movement speed (Taylor et al., 1970), mode of transport (Griffen, 2018), and
18 environmental conditions (e.g. topography, weather, substrate; Crête & Larivière, 2003; Wilson et al., 2012).
19 Environmentally-varying movement costs can be quantified in a framework known as an energy landscape,
20 which can incorporate factors such as air velocity for birds (Shepard et al., 2013), water depth for diving
21 animals (Wilson et al., 2012), or habitat type (Pagano et al., 2020). Energy landscapes are useful to quantify
22 the energetic costs of moving through heterogeneous or dynamic environments, and there are clear benefits
23 to integrating them with foraging theory.

24 Habitat selection models assess how animals distribute themselves in space relative to environmental
25 features, and therefore may be modified to assess the energetic contributions of movement decisions. Re-
26 source selection functions (RSFs) have been used to jointly estimate the effects of foraging resources and
27 energetically-costly environmental features on large-scale space-use (Long et al., 2014). However, that ap-
28 proach does not explicitly model movement, and it therefore ignores costs incurred at the scale of the
29 movement step (i.e. movement between successive recorded locations). At this scale, animals may make
30 decisions primarily based on the need to maximize energy intake, minimize energy use, or balance the two

31 (Schoener, 1971; Shepard et al., 2009; Cornioley et al., 2016). Although the idea of energy-based move-
32 ment models is not entirely new, methods remain analytically complex. For example, Hooten et al. (2019)
33 described a movement model with a binary response “recharge” function (e.g. decision to move to food
34 patch), based on a latent process for the physiological state of an animal (e.g. its satiation or cumulative
35 energy balance). A simpler, yet effective, approach could be to extend step selection functions (SSFs; i.e.
36 movement-based habitat selection models) to answer similar questions in a widely used, flexible framework.

37 In this paper, we propose an energy-based SSF, that we refer to in short-hand as the energy selection
38 function (ESF). The ESF models the effect of energetic gains and costs on an animal’s movement decisions,
39 therefore integrating movement and habitat selection in an energetic context. Mathematically, the ESF is
40 a special case of SSFs, and can be implemented using standard logistic regression software, facilitating its
41 uptake in applied studies. However, the ESF is conceptually different in defining movement and habitat
42 availability through covariates that can be explicitly linked to energetic trade-offs in decision-making. To
43 demonstrate our approach, we provide practical guidance to implement the ESF and define covariates, and
44 further outline the workflow and interpretation through an illustrative case study of polar bears (*Ursus*
45 *maritimus*) in the Beaufort Sea, Canada.

46 2 Materials and Methods

47 2.1 The ESF

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

$$51 f(\mathbf{y}|\mathbf{x}) = \frac{w(\mathbf{x}, \mathbf{y})}{\int_{\mathbf{z} \in \Omega} w(\mathbf{x}, \mathbf{z}) d\mathbf{z}}, \quad (1)$$

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

$$55 w(\mathbf{x}, \mathbf{y}) = \exp\{\beta_1 G(\mathbf{x}, \mathbf{y}) - \beta_2 C(\mathbf{x}, \mathbf{y})\}. \quad (2)$$

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

59 *against* energetic costs $C(\mathbf{x}, \mathbf{y})$, 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 $G(\mathbf{x}, \mathbf{y})$ and $C(\mathbf{x}, \mathbf{y})$ 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.

73 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 \mathbf{y} given that it started at location \mathbf{x} in the study region Ω as

$$78 f(\mathbf{y}|\mathbf{x}) = \frac{\Phi(\mathbf{y}|\mathbf{x})w(\mathbf{x}, \mathbf{y})}{\int_{\mathbf{z} \in \Omega} \Phi(\mathbf{z}|\mathbf{x})w(\mathbf{x}, \mathbf{z})d\mathbf{z}}. \quad (3)$$

79 The first term, $\Phi(\mathbf{y}|\mathbf{x})$, 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, $w(\mathbf{x}, \mathbf{y})$, is a weighting function and represents resource selection without movement constraints. The
82 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
83 representing the strength of selection for $\mathbf{h}(\mathbf{x}, \mathbf{y})$, a vector of habitat covariates. Therefore, the step density
84 of an SSF model is the product of resource selection $w(\mathbf{x}, \mathbf{y})$ and movement $\Phi(\mathbf{y}|\mathbf{x})$.

85 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
86 where $\Phi(\mathbf{y}|\mathbf{x})$ 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 $\Phi(\mathbf{y}|\mathbf{x})$ to be uniform based on the assumption

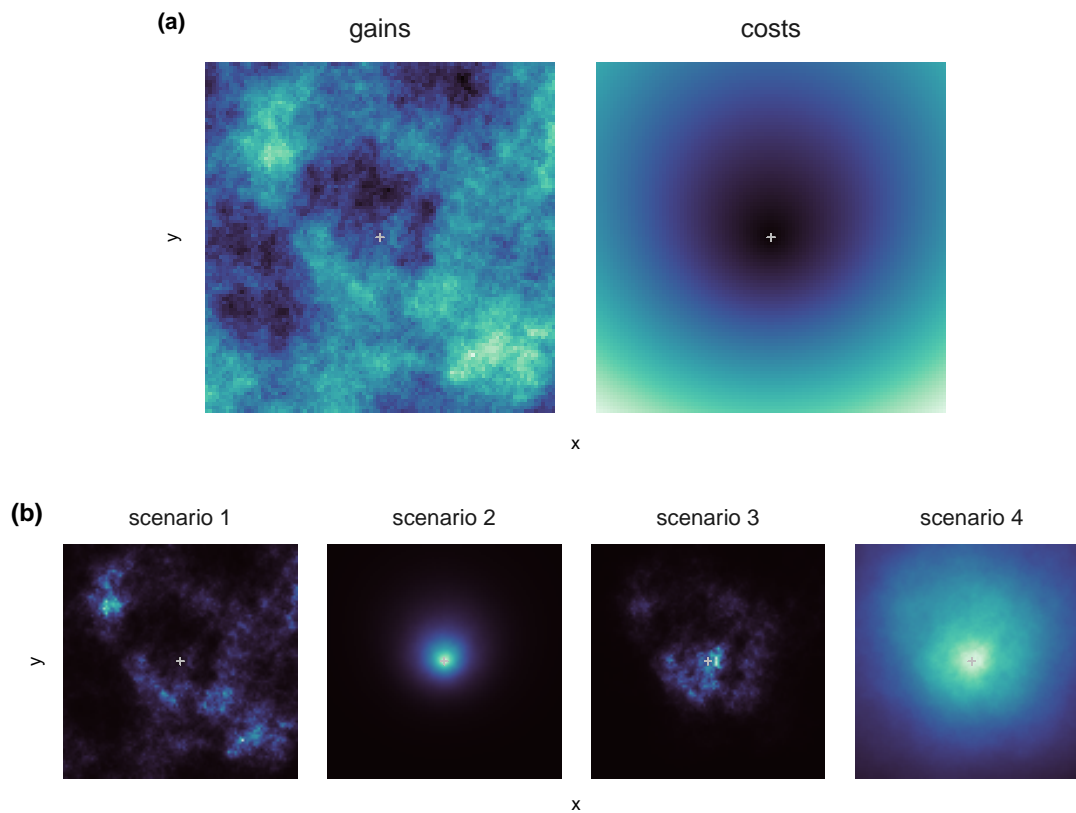


Figure 1: (a) Simulated rasters of energetic gains and energetic costs, and (b) corresponding ESFs. In (a), energetic gains were simulated as a random covariate field and energetic costs were defined as a product of the step length and turning angle from the central location (+), assuming that the animal 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_1), 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.

88 that, in the absence of energetic constraints (i.e. a hypothetical animal that can move arbitrarily fast without
 89 expending energy), animals could travel anywhere in the study region. Here, selection against costs defines
 90 a movement model, as $C(\mathbf{x}, \mathbf{y})$ can account for aspects of animal movement that affect energy expenditure
 91 (e.g. speed and tortuosity). For a simple example, in the absence of selection for gains ($\beta_1 = 0$) and if the
 92 costs are proportional to the step length squared, the ESF reduces to a Gaussian random walk with variance
 93 inversely proportional to β_2 (Appendix A). Regardless of the exact cost formulation, the ESF eliminates the
 94 need to make the assumption that availability is known, as this is captured by the selection against energetic
 95 costs. Therefore, similar to integrated step selection analysis (iSSA; Avgar et al., 2016), the ESF circumvents
 96 the difficulty of defining availability in habitat selection studies (Beyer et al., 2010), while simultaneously
 97 assessing energetic processes. For this reason, it stands in contrast with the approach of Latombe et al.
 98 (2014), where the ratio of gains over costs was included as a covariate in an SSF with a non-uniform function
 99 Φ (based on empirical distributions of step lengths and turning angles). That model measures the effects
 100 of gains and costs once movement constraints have been accounted for, rather than integrate all aspects of
 101 movement and habitat selection into energetic variables.

102 2.1.2 Implementation

103 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
 104 as $L(\beta_1, \beta_2 | \mathbf{x}_1, \dots, \mathbf{x}_n) = \prod_{i=1}^{n-1} f(\mathbf{x}_{i+1} | \mathbf{x}_i)$, where $f(\mathbf{x}_{i+1} | \mathbf{x}_i)$ is the likelihood of a single step (Equation
 105 1). In many cases, the exact likelihood is computationally intractable, as it includes the integral of w over
 106 the study region Ω . In practice, we can approximate this likelihood using a case-control (i.e. use-availability)
 107 design (Forester et al., 2009; Thurfjell et al., 2014). Case-control designs contrast habitat characteristics at
 108 locations where the animal went (i.e. what it used) with where it could have gone (i.e. available habitat),
 109 and they are common in habitat selection analyses. For each observed location \mathbf{x}_i (hereafter, a case), we
 110 generate a set of random locations (hereafter, controls) which represent a sample of the available habitat.
 111 Using Monte Carlo integration over the control locations $\{\mathbf{z}_{i1}, \mathbf{z}_{i2}, \dots, \mathbf{z}_{iK}\}$, we calculate the approximate
 112 likelihood as

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

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

115 This numerical integration requires sampling control locations $\{\mathbf{z}_{i1}, \mathbf{z}_{i2}, \dots, \mathbf{z}_{iK}\}$ from a uniform distri-
 116 bution 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 z_{ij} is sufficiently
118 far from the starting point of the step, \mathbf{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 $C(\mathbf{x}, \mathbf{y})$. 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).

134 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.

166 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.

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.

184 **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.

198 **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 Klapstein 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

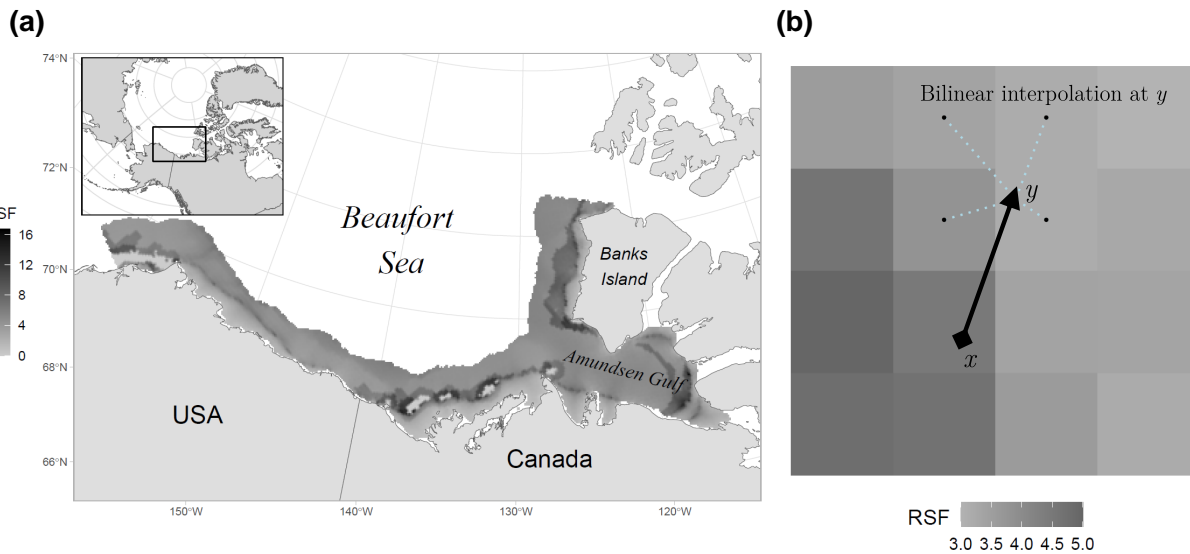


Figure 2: Illustration of energetic gains in polar bear case study. (a) Map of study area overlaid with an example of the seal biomass RSF. (b) Schematic representation of energetic gain evaluation for a step from x to y , using bilinear interpolation at y based on the four adjacent cells (black dots).

206 bear can either be swimming or walking on sea ice, which have different energetic costs (e.g. Griffen, 2018;
 207 Pagano et al., 2018). Using spring/summer (March - August) aquatic sensor data from Lone et al. (2018), we
 208 modelled the relationship between the proportion of time in water and sea ice concentration as a generalized
 209 additive model (GAM) in the *mgcv* R package (Wood, 2017). This model does not have an intercept at 1,
 210 as expected, suggesting that time spent in water may be underestimated for low ice concentration (Figure
 211 3b). This can be partially be explained by the tendency of satellites to underestimate ice concentration
 212 (e.g., Castro de la Guardia et al. 2017 found that bears were still on ice when satellite imagery indicated
 213 ice concentration of 0%). Although underestimation of time spent in water could result in conservative cost
 214 estimates, it is the best data available. Using this GAM, we estimated proportion of time spent in water for
 215 each polar bear step, based on its interpolated ice concentration value (AMSR-E 3.125 km grid Version 5.4;
 216 Spreen et al., 2008), and assumed the proportion of time in water to be the same as the proportion of the
 217 distance travelled. Lastly, we modelled the relationship between travel speed and energy expenditure, using
 218 combined estimates from five treadmill studies (Øritsland & Jonker, 1976; Hurst et al., 1982a,b; Watts et al.,
 219 1991; Pagano et al., 2018). These data included resting metabolic rates and accounted for the weight of the
 220 bear. We modelled energy expenditure as a function of walking speed as a GAM with a gamma response
 221 distribution and a positive monotonic constraint in the R package *scam* (Pya & Wood, 2015). When the bear

222 was assumed to be walking, the cost was derived directly from this curve, and when the bear was swimming,
223 we multiplied this cost by five to represent the higher energy expenditure (Griffen, 2018). Importantly, our
224 modelling approach estimated similar daily costs as those obtained from doubly-labelled water (Figure S9;
225 Pagano & Williams, 2019).

226 As suggested in Section 2.1.3, movement tortuosity (i.e. turning angle) may also affect the costs of
227 movement, and this effect could be included in analyses of high-resolution movement data (Wilson et al.,
228 2013). Although small-scale tortuosity might not appear at a 4-hour resolution, directional persistence may
229 be in place even at this coarser scale, due to large-scale targets of attraction (e.g. foraging patches, mating
230 sites), environmental features (e.g., the floe edge), or behaviours (e.g. migration, site fidelity), on which we
231 do not have sufficient information. In principle, if the energetic return of large-scale processes was known, it
232 could be captured using a multi-scale ESF similar to the approach of Bastille-Rousseau et al. (2018). Instead,
233 in Appendix F, we show how turning angle can be incorporated as a separate term in the ESF (similar to
234 Avgar et al., 2016; Brooke et al., 2020) that encapsulates in a single energy-agnostic term all the drivers
235 of directional persistence about which we do not have information, and compare this to the ESF presented
236 below.

237 2.2.3 Fitting the ESF

238 We eliminated locations that were outside the spatiotemporal extent of the seal raster (Figure 2), which
239 removed 34.1% of all locations (Figure S6). We generated 20 control locations on a disc around each
240 observed location, with radius $R = 1.1 \times l_m$, where l_m is the maximum step length of all observed locations
241 (see Appendix B for justification of R and Appendix D for number of controls). We calculated energetic
242 gains and costs of each step as described above, using environmental covariate values at each end location.
243 We omitted steps from analysis when there were ≥ 10 control locations without an energetic gain estimate
244 (i.e. outside the raster extent) and accounted for this in the ESF likelihood. We fitted the ESF with the
245 *clogit* function (from the R package *survival*) separately for each individual bear. Following Forester et al.
246 (2009), we calculated robust standard errors to account for residual autocorrelation, which can lead to the
247 underestimation of variance (details in Appendix G). We used Monte Carlo cross-validation to investigate
248 the predictive performance of the model (as described by Fortin et al., 2009, full details in Appendix H).
249 The general idea of cross-validation is to repeatedly fit the model to a random subset of the data (training
250 data set), and check how frequently it correctly distinguishes between the observed steps and control steps in
251 the remaining data (validation data set). The output of each iteration of this procedure is a Spearman rank

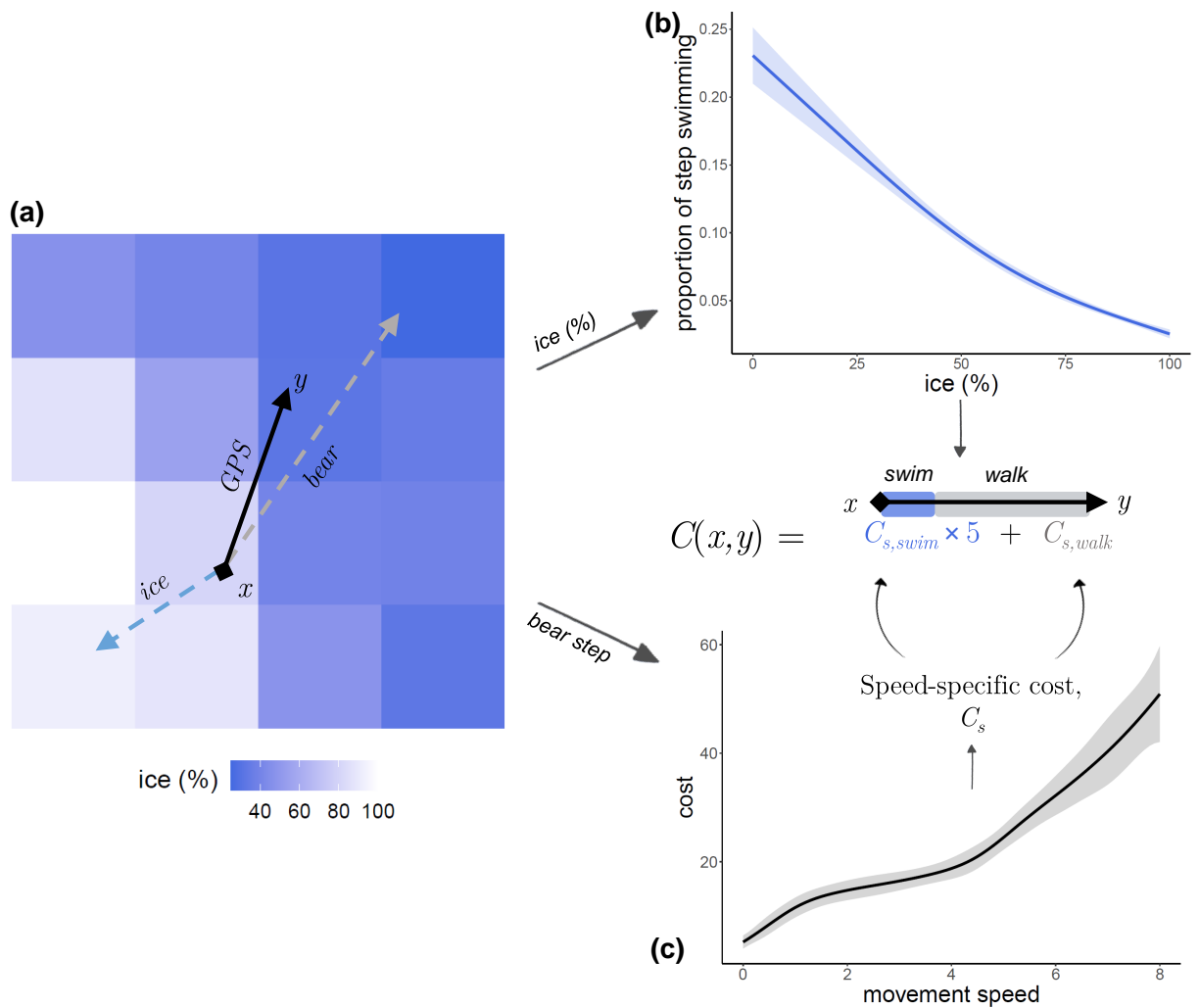


Figure 3: Schematic illustration of energetic cost evaluation in the polar bear case study, for an observed step starting at x and ending at y . (a) Arrows represent the observed movement step (black; GPS), ice drift (blue dashed; ice), and actual bear movement (grey dashed; calculated as GPS - ice). Ice concentration (%) is estimated at y with bilinear interpolation (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 $C(x, y)$ is the sum of $C_{s,swim}$ multiplied by 5 (to represent the higher costs of swimming) and $C_{s,walk}$.

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

257 **2.2.4 Comparison to an SSF**

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

276 **3 Results**

277 **3.1 ESF results**

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

280 proportional to energy), while controls had a median energetic gain of 4.3 (range: 0 – 28.1). The median
 281 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
 282 MJ (range: 3.6 – 124 MJ). The median β_1 estimate was 0.10 (range –0.32, 0.96), with three estimates with
 283 95% CIs that did not overlap zero (Figure 4). Of these, two bears appeared to select for energetic gains
 284 ($\beta_1 \pm \text{SE} = 0.42 \pm 0.14$; 0.40 ± 0.17) and one bear appeared to select against energetic gains ($\beta_1 \pm \text{SE} =$
 285 -0.32 ± 0.16). Conversely, all β_2 estimates showed a selection against costs, with a median of 0.57 (range
 286 0.27, 0.96), and no CIs overlapped zero. For every individual, cross-validation indicated that the ESF better
 287 predicted polar bear movement than what would be expected by chance (i.e. mean individual r_s was always
 288 larger for the observed than random). Across all individuals, mean r_s (range) was 0.56 (0.20, 0.89) for
 289 observed and –0.009 (–0.68, 0.77) for random. Further, we performed cross-validation on both a gain-only
 290 and a cost-only model, which showed generally low predictive power of energetic gains and higher predictive
 291 power of energetic costs (Appendix H.1).

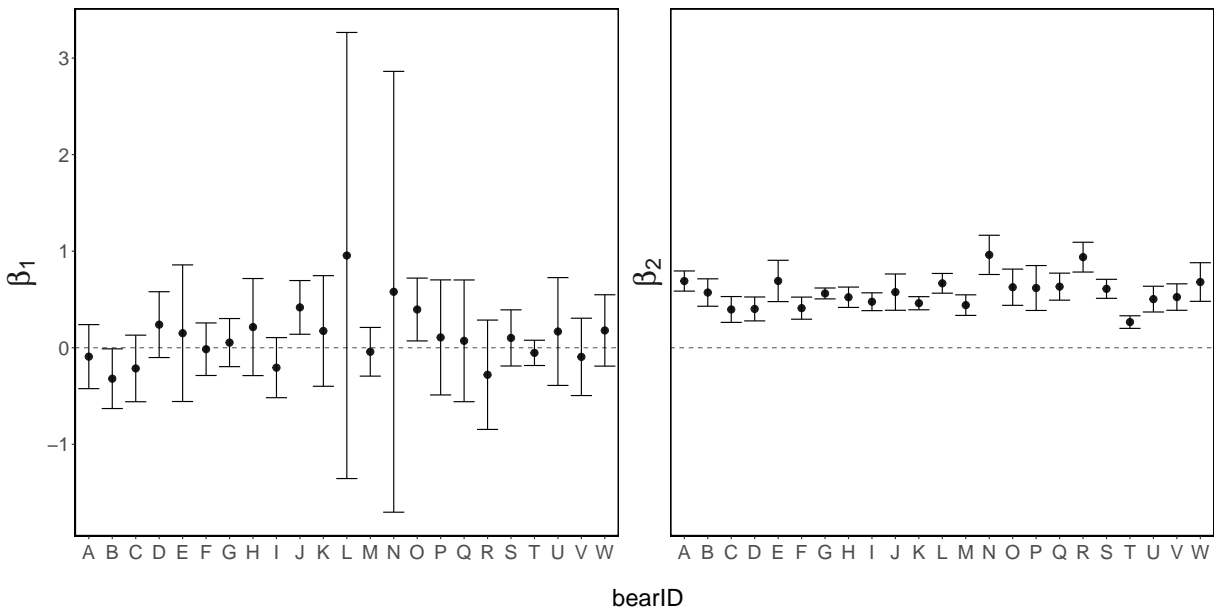


Figure 4: Estimated β_1 (selection for gains) and β_2 (selection against costs) coefficients of lone adult female polar bears ($n = 23$). Error bars are robust 95% CIs.

3.2 SSF results

293 Of the 23 individual bears, 8 had a statistically clear linear effect of ice concentration (i.e., robust 95% CIs
 294 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.

309 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.

316 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).

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

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.

364 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.

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

387 Inherently, step selection analyses are sensitive to the spatial and temporal scale of the telemetry and
388 covariate data (Munden et al., 2021). In the ESF, the spatial scale of the energetic covariates needs to be
389 fine enough that it is possible to observe preference at the scale of the observed movement steps. When
390 covariate data is coarse or spatially autocorrelated, contrast between case and control locations may be low
391 and provide little evidence of selection (Northrup et al., 2013). Another feature of step selection models
392 is that the temporal resolution of the tracking data determines the scale at which the animal's behaviour
393 is examined (Bastille-Rousseau et al., 2018). For example, selection for foraging resources at the scale of
394 the landscape (e.g. this case study) or energy accumulation over a long period (e.g. in the case of kill
395 sites) may not be apparent at the scale of finer resolution movement steps. The interpretation of the ESF
396 parameters is therefore tied to the time interval of observation, and lack of evidence for selection at the
397 movement step may not translate to a biologically relevant time-scale. Thoughtful selection of intervals
398 between telemetry locations, continuous-time analogues of SSFs, and high-frequency data may prove useful
399 to overcome these scale dependencies. We hope this study will motivate the collection of more precise data,
400 suited to understand the energetic mechanisms behind animal space use (see Williams et al., 2020, for a
401 review of available technologies).

402 The ESF has great potential for methodological extensions, due to its close theoretical and practical
403 links to existing methods (SSFs and iSSA). For example, we could consider a state-switching ESF model,
404 where an unobserved behavioural state determines the selection parameters for energetic gains and costs.
405 A state-switching ESF model would allow us to assess behaviour-specific energy selection, and could be
406 written as a hidden Markov model, similar to the state-switching SSF model of Nicosia et al. (2017). It may
407 also be possible to incorporate temporal dynamics and energetic state (e.g. satiation or cumulative energy
408 balance; Latombe et al., 2014) to better reflect the physiological demands and constraints of gaining energy
409 (i.e. recharge dynamics; Hooten et al., 2019). Further, it should be straightforward to include non-energetic
410 terms (e.g., associated with predator risk) as interactions with gains and costs to assess how animals make
411 energetic trade-offs with other aspects of survival. Here, we presented a re-imagining of SSFs, in which we
412 use energy to summarise both habitat selection and movement. This approach is widely applicable, flexible
413 enough to include a range of extensions, and can ultimately be used to build on foraging and movement
414 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).

References

- Arthur, S.M., Manly, B.F.J., Mcdonald, L.L. & Garner, G.W. (1996). Assessing habitat selection when availability changes. *Ecology*, *77*, 215–227.
- Avgar, T., Potts, J.R., Lewis, M.A. & Boyce, M.S. (2016). Integrated step selection analysis: bridging the gap between resource selection and animal movement. *Methods in Ecology and Evolution*, *7*, 619–630. <https://doi.org/10.1111/2041-210X.12528>
- Bastille-Rousseau, G., Murray, D.L., Schaefer, J.A., Lewis, M.A., Mahoney, S.P. & Potts, J.R. (2018). Spatial scales of habitat selection decisions: implications for telemetry-based movement modelling. *Ecography*, *41*, 437–443. <https://doi.org/10.1111/ecog.02655>
- Bastille-Rousseau, G., Wall, J., Douglas-Hamilton, I., Lesowapir, B., Loloju, B., Mwangi, N. & Wittemyer, G. (2020). Landscape-scale habitat response of African elephants shows strong selection for foraging opportunities in a human dominated ecosystem. *Ecography*, *43*, 149–160. <https://doi.org/10.1111/ecog.04240>
- Beyer, H.L., Haydon, D.T., Morales, J.M., Frair, J.L., Hebblewhite, M., Mitchell, M. & Matthiopoulos, J. (2010). The interpretation of habitat preference metrics under use-availability designs. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*, 2245–2254. <https://doi.org/10.1098/rstb.2010.0083>
- Bidder, O.R., Goulding, C., Toledo, A., Van Walsum, T.A., Siebert, U. & Halsey, L.G. (2017). Does the treadmill support valid energetics estimates of field locomotion? *Integrative and Comparative Biology*, *57*, 301–319. <https://doi.org/10.1093/icb/ix038>
- Boyce, M.S. (2006). Scale for resource selection functions. *Diversity and Distributions*, *12*, 269–276. <https://doi.org/10.1111/j.1366-9516.2006.00243.x>
- Boyce, M.S., Mao, J.S., Merrill, E.H., Fortin, D., Turner, M.G., Fryxell, J. & Turchin, P. (2003). Scale and heterogeneity in habitat selection by elk in Yellowstone National Park. *Ecoscience*, *10*, 421–431. <https://doi.org/10.1080/11956860.2003.11682790>
- Brooke, C.F., Fortin, D., Kraaij, T., Fritz, H., Kalule-Sabiti, M.J. & Venter, J.A. (2020). Poaching impedes the selection of optimal post-fire forage in three large grazing herbivores. *Biological Conservation*, *241*, 108393. <https://doi.org/10.1016/j.biocon.2019.108393>
- Castro de la Guardia, L., Myers, P.G., Derocher, A.E., Lunn, N.J. & Terwisscha van Scheltinga, A.D. (2017). Sea ice cycle in western Hudson Bay, Canada, from a polar bear perspective. *Marine Ecology Progress Series*, *564*, 225–233. <https://doi.org/10.3354/meps11964>
- Cornioley, T., Börger, L., Ozgul, A. & Weimerskirch, H. (2016). Impact of changing wind conditions on foraging and incubation success in male and female wandering albatrosses. *Journal of Animal Ecology*, *85*, 1318–1327. <https://doi.org/10.1111/1365-2656.12552>
- Crête, M. & Larivière, S. (2003). Estimating the costs of locomotion in snow for coyotes. *Canadian Journal of Zoology*, *81*, 1808–1814. <https://doi.org/10.1139/Z03-182>
- Duparc, A., Garel, M., Marchand, P., Dubray, D., Maillard, D. & Loison, A. (2020). Through the taste buds of a large herbivore: foodscape modeling contributes to an understanding of forage selection processes. *Oikos*, *129*, 170–183. <https://doi.org/10.1111/oik.06386>
- Durner, G.M., Douglas, D.C., Albeke, S.E., Whiteman, J.P., Amstrup, S.C., Richardson, E.S., Wilson, R.R. & Ben-David, M. (2017). Increased Arctic sea ice drift alters adult female polar bear movements and energetics. *Global Change Biology*, *23*, 3460–3473. <https://doi.org/10.1111/gcb.13746>

- Eisaguirre, J.M., Booms, T.L., Barger, C.P., Lewis, S.B. & Breed, G.A. (2020). Novel step selection analyses on energy landscapes reveal how linear features alter migrations of soaring birds. *Journal of Animal Ecology*, *89*, 2567–2583. <https://doi.org/10.1111/1365-2656.13335>
- Forester, J., Kyung Im, H. & Rathouz, P. (2009). Accounting for animal movement in estimation of resource selection functions: sampling and data analysis. *Ecology*, *90*, 3554–3565. <https://doi.org/10.1890/08-0874.1>
- Fortin, D., Fortin, M.E., Beyer, H.L., Duchesne, T., Courant, S. & Dancose, K. (2009). Group-size-mediated habitat selection and group fusion – fission dynamics of bison under predation risk. *Ecology*, *90*, 2480–2490.
- Fortin, D., Fryxell, J.M., O’brodovich, L. & Frandsen, D. (2003). Foraging ecology of bison at the landscape and plant community levels: the applicability of energy maximization principles. *Oecologia*, *134*, 219–227. <https://doi.org/10.1007/s00442-002-1112-4>
- Fryxell, J.M. (1997). Evolutionary dynamics of habitat use. *Evolutionary Ecology*, *11*, 687–701. <https://doi.org/10.1023/A:1018434302138>
- Griffen, B.D. (2018). Modeling the metabolic costs of swimming in polar bears (*Ursus maritimus*). *Polar Biology*, *41*, 491–503. <https://doi.org/10.1007/s00300-017-2209-x>
- Halsey, L.G. (2016). Terrestrial movement energetics: current knowledge and its application to the optimising animal. *Journal of Experimental Biology*, *219*, 1424–1431. <https://doi.org/10.1242/jeb.133256>
- Hooten, M.B., Scharf, H.R. & Morales, J.M. (2019). Running on empty: recharge dynamics from animal movement data. *Ecology Letters*, *22*, 377–389. <https://doi.org/10.1111/ele.13198>
- Hurst, R.J., Leonard, M.L., Watts, P.D., Beckerton, P. & Øritsland, N.a. (1982a). Polar bear locomotion: body temperature and energetic cost. *Canadian Journal of Zoology*, *60*, 40–44. <https://doi.org/10.1139/z82-005>
- Hurst, R.J., Øritsland, N.A. & Watts, P. (1982b). Body mass, temperature and cost of walking in polar bears. *Acta Physiologica Scandinavica*, *115*, 391–395. <https://doi.org/10.1111/j.1748-1716.1982.tb07096.x>
- Jakobsson, M., Jakobsson, M., Mayer, L.A., Bringensparr, C., Castro, C.F., Mohammad, R., Johnson, P., Ketter, T., Accettella, D., Amblas, D., An, L., Arndt, J.E., Canals, M., Casamor, J.L., Chauche, N., Coakley, B., Danielson, S., Demarte, M., Dickson, M.L., Dorschel, B., Dowdeswell, J.A. & Dreutter, S. (2020). The International Bathymetric Chart of the Arctic Ocean Version. *Scientific Data*, p. 176. <https://doi.org/10.1038/s41597-020-0520-9>
- Johnson, A.C. & Derocher, A.E. (2020). Variation in habitat use of Beaufort Sea polar bears. *Polar Biology*, *43*, 1247–1260. <https://doi.org/10.1007/s00300-020-02705-3>
- Kays, R., Crofoot, M.C., Jetz, W. & Wikelski, M. (2015). Terrestrial animal tracking as an eye on life and planet. *Science*, *348*, aaa2478. <https://doi.org/10.1126/science.aaa2478>
- Klappstein, N.J., Potts, J.R., Michelot, T., Börger, L., Pilfold, N.W., Lewis, M.A. & Derocher, A.E. (2022). Reproducing the analyses of the article “Energy-based step selection analysis: modelling the energetic drivers of animal movement and habitat use”. *Zenodo*. <https://doi.org/https://doi.org/10.5281/zenodo.6319709>
- Klappstein, N.J., Togunov, R.R., Reimer, J.R., Lunn, N.J. & Derocher, A.E. (2020). Patterns of sea ice drift and polar bear (*Ursus maritimus*) movement in Hudson Bay. *Marine Ecology Progress Series*, *641*, 227–240. <https://doi.org/10.3354/meps13293>
- Latombe, G., Parrott, L., Basille, M. & Fortin, D. (2014). Uniting statistical and individual-based approaches for animal movement modelling. *PLOS ONE*, *9*, e99938. <https://doi.org/10.1371/journal.pone.0099938>

- Lone, K., Kovacs, K.M., Lydersen, C., Fedak, M., Andersen, M., Lovell, P. & Aars, J. (2018). Aquatic behaviour of polar bears (*Ursus maritimus*) in an increasingly ice-free Arctic. *Scientific Reports*, 8, 9677. <https://doi.org/10.1038/s41598-018-27947-4>
- Long, R.A., Terry Bowyer, R., Porter, W.P., Mathewson, P., Monteith, K.L. & Kie, J.G. (2014). Behavior and nutritional condition buffer a large-bodied endotherm against direct and indirect effects of climate. *Ecological Monographs*, 84, 513–532. <https://doi.org/10.1890/13-1273.1>
- Mauritzen, M., Derocher, A.E. & Wiig, Ø. (2001). Space-use strategies of female polar bears in a dynamic sea ice habitat. *Canadian Journal of Zoology*, 79, 1704–1713. <https://doi.org/10.1139/z01-126>
- McCall, A.G., Pilfold, N.W., Derocher, A.E. & Lunn, N.J. (2016). Seasonal habitat selection by adult female polar bears in western Hudson Bay. *Population Ecology*, 58, 407–419. <https://doi.org/10.1007/s10144-016-0549-y>
- Merkle, J.A., Fortin, D. & Morales, J.M. (2014). A memory-based foraging tactic reveals an adaptive mechanism for restricted space use. *Ecology Letters*, 17, 924–931. <https://doi.org/10.1111/ele.12294>
- Michelot, T., Blackwell, P.G. & Matthiopoulos, J. (2019). Linking resource selection and step selection models for habitat preferences in animals. *Ecology*, 100, e02452. <https://doi.org/10.1002/ecy.2452>
- Munden, R., Börger, L., Wilson, R.P., Redcliffe, J., Brown, R., Garel, M. & Potts, J.R. (2021). Why did the animal turn? Time-varying step selection analysis for inference between observed turning points in high frequency data. *Methods in Ecology and Evolution*. <https://doi.org/10.1111/2041-210x.13574>
- Nicosia, A., Duchesne, T., Rivest, L.P. & Fortin, D. (2017). A multi-state conditional logistic regression model for the analysis of animal movement. *The Annals of Applied Statistics*, 11, 1537–1560. <https://doi.org/10.1214/17-AOAS1045>
- Northrup, J.M., Hooten, M.B., Anderson, C.R.J. & Wittemyer, G. (2013). Practical guidance on characterizing availability in resource selection functions under a use-availability design. *Ecology*, 94, 1456–1463. <https://doi.org/10.1890/12-1688.1>
- Øritsland, N. & Jonker, W. (1976). A respiration chamber for exercising polar bears. *Norwegian Journal of Zoology*, 24, 65–67.
- Owen-Smith, N., Fryxell, J.M. & Merrill, E.H. (2010). Foraging theory upscaled: the behavioural ecology of herbivore movement. *Philosophical Transactions of the Royal Society Series B: Biological Sciences*, 365, 2267–2278. <https://doi.org/10.1098/rstb.2010.0095>
- Pagano, A.M., Atwood, T.C., Durner, G.M. & Williams, T.M. (2020). The seasonal energetic landscape of an apex marine carnivore, the polar bear. *Ecology*, 101, e02959. <https://doi.org/10.1002/ecy.2959>
- Pagano, A.M., Durner, G.M., Rode, K.D., Atwood, T.C., Atkinson, S.N., Peacock, E., Costa, D.P., Owen, M.A. & Williams, T.M. (2018). High-energy, high-fat lifestyle challenges an Arctic apex predator, the polar bear. *Science*, 359, 568–572. <https://doi.org/10.1126/science.aan8677>
- Pagano, A.M. & Williams, T.M. (2019). Estimating the energy expenditure of free-ranging polar bears using tri-axial accelerometers: A validation with doubly labeled water. *Ecology and Evolution*, 9, 4210–4219. <https://doi.org/10.1002/ece3.5053>
- Pilfold, N.W., Derocher, A.E. & Richardson, E.S. (2014). Influence of intraspecific competition on the distribution of a wide-ranging, non-territorial carnivore. *Global Ecology and Biogeography*, 23, 425–435. <https://doi.org/10.1111/geb.12112>
- Pilfold, N.W., Derocher, A.E., Stirling, I., Richardson, E.S. & Andriashek, D.S. (2012). Age and sex composition of seals killed by polar bears in the Eastern Beaufort Sea. *PLoS ONE*, 7, e41429. <https://doi.org/10.1371/journal.pone.0041429>

- Potts, J.R., Bastille-Rousseau, G., Murray, D.L., Schaefer, J.A. & Lewis, M.A. (2014). Predicting local and non-local effects of resources on animal space use using a mechanistic step selection model. *Methods in Ecology and Evolution*, 5, 253–262. <https://doi.org/10.1111/2041-210X.12150>
- Pyra, N. & Wood, S.N. (2015). Shape constrained additive models. *Statistics and Computing*, 25, 543–559. <https://doi.org/10.1007/s11222-013-9448-7>
- Pyke, G.H. (2019). Animal movements - an optimal foraging theory approach. *Encyclopedia of Animal Behavior*, volume 2, pp. 149–156. Elsevier, second edition. <https://doi.org/10.1016/B978-0-12-809633-8.90160-2>
- Pyke, G.H., Pulliam, H.R. & Charnov, E.L. (1977). Optimal foraging: A selective review of theory and tests. *The Quarterly Review of Biology*, 52, 137–154.
- Ramsay, M.A. & Stirling, I. (1986). On the mating system of polar bears. *Canadian Journal of Zoology*, 64, 2142–2151. <https://doi.org/10.1139/z86-329>
- Schoener, T.W. (1971). Theory of feeding strategies. *Annual Review of Ecology and Systematics*, 2, 369–404. <https://doi.org/10.1146/annurev.es.02.110171.002101>
- Shepard, E.L.C., Wilson, R.P., Quintana, F., Gó Mez Laich, A. & Forman, D.W. (2009). Pushed for time or saving on fuel: fine-scale energy budgets shed light on currencies in a diving bird. *Proceedings of the Royal Society B*, 276, 3149–3155. <https://doi.org/10.1098/rspb.2009.0683>
- Shepard, E.L.C., Wilson, R.P., Rees, W.G., Grundy, E., Lambertucci, S.A. & Vosper, S.B. (2013). Energy landscapes shape animal movement ecology. *The American Naturalist*, 182, 298–312. <https://doi.org/10.1086/671257>
- Spreen, G., Kaleschke, L. & Heygster, G. (2008). Sea ice remote sensing using AMSR-E 89-GHz channels. *Journal of Geophysical Research: Oceans*, 113, C02S03. <https://doi.org/10.1029/2005JC003384>
- Stirling, I., Spencer, C. & Andriashek, D. (2016). Behavior and activity budgets of wild breeding polar bears (*Ursus maritimus*). *Marine Mammal Science*, 32, 13–37. <https://doi.org/10.1111/mms.12291>
- Taylor, C.R., Schmidt-Nielsen, K. & Raab, J.L. (1970). Scaling of energetic cost of running to body size in mammals. *The American Journal of Physiology*, 219, 1104–1107. <https://doi.org/10.1152/ajplegacy.1970.219.4.1104>
- Thurfjell, H., Ciuti, S. & Boyce, M.S. (2014). Applications of step-selection functions in ecology and conservation. *Movement Ecology*, 4, 1–12. <https://doi.org/10.1186/2051-3933-2-4>
- Tschudi, M., Meier, W.N., Stewart, J.S., Fowler, C. & Maslanik, J. (2019). Polar Pathfinder Weekly 25 km EASE-Grid Sea Ice Motion Vectors, Version 4, Northern Hemisphere.
- Watts, P., Ferguson, K.L. & Draper, B. (1991). Energetic output of subadult polar bears (*Ursus maritimus*): Resting, disturbance and locomotion. *Comparative Biochemistry and Physiology*, 98A, 191–193. [https://doi.org/10.1016/0300-9629\(91\)90518-H](https://doi.org/10.1016/0300-9629(91)90518-H)
- Williams, T.M., Peter-Heide Jørgensen, M., Pagano, A.M. & Bryce, C.M. (2020). Hunters versus hunted: New perspectives on the energetic costs of survival at the top of the food chain. *Functional Ecology*, 34, 2015–2029. <https://doi.org/10.1111/1365-2435.13649>
- Wilson, R.P., Griffiths, I.W., Legg, P.A., Friswell, M.I., Bidder, O.R., Halsey, L.G., Lambertucci, S.A. & Shepard, E.L.C. (2013). Turn costs change the value of animal search paths. *Ecology Letters*, 16, 1145–1150. <https://doi.org/10.1111/ele.12149>

- Wilson, R.P., Börger, L., Holton, M.D., Scantlebury, D.M., Gómez-Laich, A., Quintana, F., Rosell, F., Graf, P.M., Williams, H., Gunner, R., Hopkins, L., Marks, N., Geraldi, N.R., Duarte, C.M., Scott, R., Strano, M.S., Robotka, H., Eizaguirre, C., Fahlman, A. & Shepard, E.L. (2020). Estimates for energy expenditure in free-living animals using acceleration proxies: A reappraisal. *Journal of Animal Ecology*, 89, 161–172. <https://doi.org/10.1111/1365-2656.13040>
- Wilson, R.P., Quintana, F. & Hobson, V.J. (2012). Construction of energy landscapes can clarify the movement and distribution of foraging animals. *Proceedings of the Royal Society B*, 279, 975–980. <https://doi.org/10.1098/rspb.2011.1544>
- Wood, S.N. (2017). *Generalized Additive Models: An Introduction with R*. Chapman and Hall/CRC, 2nd edition.