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1 **Energy landscapes and the landscape of fear**

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10

11 **Abstract**

12 Animals are not distributed randomly in space and time because their movement ecology is
13 influenced by a variety of factors. Energy landscapes and the landscape of fear have recently
14 emerged as largely independent paradigms, both re-shaping our perspectives and thinking about
15 the spatial ecology of animals across heterogeneous landscapes. We argue that these paradigms
16 are not distinct but rather complementary, collectively providing a better mechanistic basis for
17 understanding the spatial ecology and decision-making of wild animals. We discuss the
18 theoretical underpinnings of each paradigm and illuminate the complementary nature through
19 case studies, then integrate these concepts quantitatively by constructing models of movement
20 pathways modulated by energy and fear to elucidate the mechanisms underlying the spatial
21 ecology of wild animals.

22

23 **Keywords:** animal ecology; energy, fear, predators, movement

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28 **The mechanistic basis of animal movement**

29 The collective storing and interpretation of environmental information is a fundamental
30 component of daily life at virtually all levels of organismal function and biological organization.
31 For animals, this integration of information over time and space feeds into a complex decision-
32 making process that drives behavioral changes critical to survival and fitness. The interest in this
33 decision-making process, specifically as it relates to the ability to understand how animals move
34 and are distributed through time and space, has fueled the study of animal ecology dating back to
35 questions posed by Aristotle nearly 2,300 years ago [1].

36 It is clear that animal movement, and therefore animal space use, is affected by factors
37 such as predation [2], food distribution [3] and social interactions [4] , and Darwinian natural
38 selection explains why. Perhaps the most discussed driver for animal movement is foraging.
39 Indeed, judicious harvesting of energy during foraging is what spawned the numerous
40 publications on optimal foraging dating back to the 1970s where workers began by manipulating
41 and controlling resources in the laboratory [5]. The optimal foraging framework led to critical
42 conceptual advances in animal movement studies such as ‘giving up time’ and optimized ‘central
43 place foraging’ which have since been applied to studies in the wild [3], changing the way the
44 biological community thought about animal movement and prey selection [6].

45 But this approach, whilst providing an elegant framework for dealing with energy
46 acquisition, generally oversimplified environmentally dependent criteria, now considered
47 important for animal decision-making, such as energy loss during the very movement that is so
48 critical for resource acquisition [7], or exposure to predation risk. These omissions can limit the
49 explanatory power of the approach because movement costs are highly variable (e.g., due to
50 physical properties of the environment) and typically involve among the greatest energy

51 expenditures of animals [8][10], and it is now clear that the risk of predation can also structure
52 how animals use their landscapes [2,9]

53 The fact that important attributes of landscapes vary in both space and time has been the
54 central tenet of two separate and divergent research themes, both of which are today receiving
55 increasing attention in the research communities studying wild animal biology and ecology;
56 energy landscapes and the landscape of fear [2,10]. With respect to energy landscapes, recent
57 work has highlighted that the characteristics of the environment through which an animal moves,
58 irrespective of whether it is water, air or over ground, profoundly affect the power use of the
59 moving animal and therefore the costs of movement per meter travelled (the costs of transport)
60 [10,11]. The landscape of fear, on the other hand, is grounded in the controlling effects predators
61 can have on prey, which trigger food vs. risk trade-offs which can change animal behavior
62 including movement [12,13]. Theory and methodological innovation (e.g., biotelemetry and
63 biologging) are at the core of both research themes. While they are both believed to have great
64 power in the ability to predict animal movement, each seems to be moving independently in
65 different directions although they should be integrated together to represent the real world. Here,
66 we propose to merge concepts central to energy landscapes with those relevant to the landscape
67 of fear to provide a framework that enhances our ability to understand how animals are
68 distributed in space and time. We briefly discuss the theoretical, biological, and ecological
69 underpinnings of both research themes, and illustrate the justification for their integration
70 through two real-world ecological examples. We then operationalize this idea by constructing
71 models of movement pathways modulated by energy and fear in hopes that our framework can
72 be used to calculate the amount of extra energy an animal is willing to spend to avoid predators
73 (i.e., the cost of predation risk and danger) [14] based on animal movement data. We hope that

74 this framework will demonstrate potential for better understanding of why animals move and
75 how they are distributed in space and time.

76 **Energy landscapes**

77 The costs of movement depend on the environment through which an animal moves.
78 Although studies examining animal movement during migration have emphasized the
79 importance of barriers and flow streams (in air and water) in modulating movement [15,16], few
80 have demonstrated the role that these variable energy costs play in animal space use and
81 movement on a day to day basis [15,17]. Indeed, Dickenson et al. [18] note that determinations
82 of the costs of locomotion in a laboratory setting are unlikely to be applicable to the wild.
83 Unsurprisingly, therefore, where authors have examined how natural environments affect the
84 cost of locomotion, the variation in energy expenditure with environment type is impressive. For
85 example, we know that humans walking on ‘soft sand’ require 2.1-2.7 times more energy than on
86 solid rock [19,20] and that people walking up slopes experience an increase in cost of transport
87 with slope angle such that a man walking up a 45° slope expends 17 times more energy per
88 metre than walking on the flat [21]. Similarly, a bird flying into a wind at the speed of the wind
89 has infinite travel costs while if that same bird flies with the wind, it will have transport costs it
90 would have in still air.

91 So, given the ability to allude to the interaction between space, movement, energy
92 expenditure and behaviour in free-living animals, what might be expected for animals having to
93 operate in variable energy landscapes? Using an optimality approach, animals should respond to
94 energy landscapes to optimize energy expenditure over all time scales, for example on an hour to
95 hour or day to day basis, and their movement should reflect this.

96 A generalized solution for the movement costs (EE) between any two points can be represented
97 by:

$$98 \quad EE = \int P dt \quad (1)$$

99 Where P = power. More properly though, power use would also be a function of the energy
100 landscape and routine metabolic rate (RMR), ϵ , so that

$$101 \quad P = RMR + f(\epsilon) \quad (2)$$

102 If, other things being equal, animals attempted to minimize travelling costs between two points,
103 we would expect them to display a trajectory where the sum costs of all speeds and turns of the
104 chosen trajectory across the different energy landscapes were minimized (EE_{min}) so that;

$$105 \quad EE_{min} = argmin_p [\int_{t_0}^{t_n} RMR + f(\epsilon) dt] \quad (3)$$

106 Here, the set of all possible paths through the landscape is represented by the set P . The
107 minimization cost function adds the resting metabolic cost (RMR) to the energy landscape cost
108 (ϵ) at all points along each path (from the beginning at t_0 to the end at t_n , the limits on the
109 integration). The path with the lowest total value is the minimum cost path.

110 The formulation above provides a framework with which putative animal movement may
111 be determined according to only one element though – energy. In addition, movement
112 trajectories will depend on other things, notably the distribution of resources and the probability
113 of being predated.

114 **The landscape of fear**

115 In its initial representation, the ‘landscape of fear’ was based on predators eliciting, in
116 their prey, a fear of being killed (the risk of predation) throughout the ecosystem [2]. These ‘fear
117 effects’ can significantly alter the physiology, behavior, and life-history of prey species [22].

118 This “ecology of fear” is increasingly being recognized as crucial in understanding the role of
119 predators, the mechanics of predator-prey interactions, and even the ecosystem-wide
120 consequences of removing predators from natural systems [23]. It has been proposed that the
121 spatial and temporal manner in which wild animals utilize their landscapes is *fear driven*, and
122 that it permeates all areas of animal ecology [24]. This natural game of cat-and-mouse between
123 predators and their prey affects how both groups navigate their landscapes. This “landscape of
124 fear” interaction, which integrates concepts from psychology, neuroscience, ecology, and bio-
125 geography [2] is thought to drive direct changes in prey distribution and, consequently, indirect
126 changes in lower trophic level resources. Thus, the landscape of fear acts as a buffer to lower
127 trophic levels from over-consumption by other consumers (usually herbivores), and it has been
128 linked to the occurrence of trophic cascades [25]. A well-known example of this concept is the
129 reintroduction of wolves in Yellowstone National Park, whereby the re-insertion of the fear of
130 mortality by wolves has been correlated with changes in elk reproductive fitness, decreases in elk
131 populations, and dramatic changes in the structure of the natural landscapes [12,26–29].

132 Predator ecologists have suggested that failing to consider the landscape of fear will
133 underestimate the effect that large carnivores play. While this concept is well-established in the
134 ecological community, the costs of the risk of predation are rarely quantified beyond food-risk
135 mesocosm-based approaches [14] or correlations, and they tend to be an inferred construct of the
136 effects of predation risk on prey.

137 Beyond this though, we suggest that the landscape of fear should also be expanded
138 beyond the risk of being predated to any space-linked process that may lead to death in a
139 probabilistic sense. Examples include environmentally challenging terrains, such as cliffs for
140 ungulates, or downdraughts for birds, whose value may also change over time, and there is no α

141 *priori* reason why such phenomena should not be treated within the same framework.
142 Nevertheless, we concentrate our discourse on ‘fear’ being used to describe the fear of being
143 killed because, while we know that the risk of being killed in a general sense can affect animal
144 movements (particularly large vertebrates), our understanding of how it actually changes their
145 distribution in space and time is lacking [30,31].

146 Given the above, the landscape of fear remains rather vaguely described, particularly as it
147 related to how species navigate their landscapes. Integrating separate, yet complementary
148 concepts surrounding animal decision-making should provide a more holistic understanding of
149 how energy and fear drive the distribution of free-ranging animals. Here, we present a series of
150 real-world, well-studied examples that empirically demonstrate the integration of both energy
151 landscapes and the landscape of fear (i.e., the risk of being killed). We then provide a
152 hypothetical example for quantifying them together to enhance our understanding of animal
153 distribution.

154 **Intersections between energy and risk in the wild**

155 While it is common to refer to ‘the landscape of fear’ to describe the constraints that
156 predation risk can create, it is often debatable whether fear or stress are involved, although it is
157 often clear that energetic effects are central to the costs of avoiding predation. Energetic or
158 nutritional costs driven by trade-offs between vigilance and foraging are well described (and
159 often important), but avoiding predation, for example, can influence energetics in less obvious
160 ways.

161 To illustrate intersections between risk and energetics with consequences for the
162 distribution and abundance of a species, consider the African wild dog (*Lycaon pictus*). Wild

163 dogs commonly prey on species like wildebeest (*Connochaetes taurinus*), warthog (*Phacocoerus*
164 *africanus*), gazelles (*Gazella* spp.) and impala (*Aepyceros melampus*) that are important prey for
165 much larger carnivores including lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*)
166 (*Crocuta crocuta*) [32–34], and this dietary overlap creates the potential for interspecific
167 competition [35–37]. The energetic costs of catching and killing ungulate prey are substantial
168 [38], which creates an additional selection pressure favoring kleptoparasitism, even if live prey
169 are not in limited supply. Consequently, hyenas sometimes follow wild dogs while they are
170 hunting (even before they make a kill) and where hyenas are abundant and visibility is good,
171 hyenas displace wild dogs at up to 86% of their kills [35,39], although the rate of
172 kleptoparasitism by hyenas varies 43-fold among published studies [40]). These food losses by
173 wild dogs must be offset by increasing the energy invested in finding, catching and killing prey,
174 which is substantial even without losses to scavengers [38,41]

175 Moreover, the behavioral and morphological adaptations of large carnivores make the
176 consequences of interference competition potentially severe, and conflict with lions is a common
177 cause of death for wild dogs [36,42,43]. As a consequence, wild dogs avoid lions at all spatio-
178 temporal scales (Fig. 1). At the finest scale, the most common response of wild dogs to nearby
179 lion roars is to stop, reverse direction and rapidly move several kilometers away. At the scale of
180 entire ecosystems, wild dog densities are low where lion (and hyena) densities are high [35,42].
181 At intermediate scales, wild dogs consistently avoid areas that are heavily used by lions (Fig.1)
182 [35,36,44] and in the Selous Game Reserve, this avoidance of lions has caused wild dogs to hunt
183 most often in deciduous woodland, where their rates of encounter with prey (3.8 prey
184 animals/km moved) are substantially lower than in habitats preferred by lions (9.9 prey
185 animals/km moved) (Fig. 1).

186 But these data only show that lions and spotted hyenas limit wild dogs in large part by
187 energetic mechanisms such as food loss, reduced rates of prey encounter, forced changes in
188 travel routes and rapid avoidance movements. We speculate that movement-related energetic
189 consequences of risk avoidance are highly likely to exist beyond this, not least because the
190 environment is different, affecting power costs for movement in a more subtle manner. For
191 example, prey pursuit of prey by wild dogs in deciduous woodland will necessarily involve a
192 more tortuous path than on the open grasslands, with correspondingly increased power use due to
193 the substantial energetic costs of turning [45]. Such effects, summed over several hunts per day
194 and 365 days per year, could have appreciable effects on fitness.

195 Field studies using GPS collars are beginning to quantify these more subtle interactions
196 between risk and energy (Fig. 2). For example, in a landscape with a mosaic of grassland and
197 forest, the presence of wolves caused elk to shift from preferred foraging habitat in meadows to
198 the protective cover of forests, but in a manner that produced relatively little change in elevation,
199 slope or speed of travel [46]. This reveals that even strong habitat shifts in response to risk can
200 be sensitive to the costs of movement. Even more subtly, foraging locations used by elk were
201 strongly related to snow depth and density when wolves were absent, but not when wolves were
202 present [47]. Because the costs of locomotion and digging for food depend on snow depth and
203 condition, this represents an important interaction between the landscapes of energy and risk
204 (Fig. 2).

205 To summarize, the costs of antipredator responses are often strongly tied to energetics. A
206 better understanding of this intersection will require simultaneous attention to measurements of
207 risk, foraging success [14] and energy expenditure.

208

209 **Box 1. Fear and energy landscapes integrated in mid-air: Herring gulls**

210 Like all soaring birds, Herring gulls *Larus argentatus* can accrue great energetic savings
211 by selectively flying in areas with rising air that allows them to glide rather than flap, so it is
212 little surprise that their medium scale movement is partly modulated by the distribution of this
213 lift. However, examining flight trajectories over a fine scale, Shepard et al. [48] have shown that
214 gulls using lift generated by onshore winds hitting seafront hotels do not position themselves in
215 the positions of highest lift, which is immediately adjacent to the buildings. Instead, they fly
216 some 10-20 m away, where the collision risk is reduced but where they can still gain from the,
217 albeit reduced, orographic lift. Data presented in the work by Shepard et al. [48] allow some
218 simple calculations to see the extent to which the risk is traded for energy so that energy losses
219 can be equated directly with distances to life-threatening features within the environment (see
220 Box 1 caption for further text).

221 **Integrating concepts**

222 We propose that we can use least cost pathways within the energy landscape as a
223 mechanism with which to quantify landscape effects because non-concordance of trajectories
224 with a minimal cost solution would indicate prioritization to other aspects, such as reducing the
225 risk of predation. Specifically, the extent of deviations from the minimum path should help our
226 understanding of movement driver hierarchies with the difference in cost between the least cost
227 pathway and that chosen being attributable to the landscape of fear, or indeed any other
228 constraint (Fig. 3).

229

230

231 **Conclusion**

232 Animal ecology has become increasingly mechanistic in recent years, with researchers
233 applying different paradigms to understand how animals are distributed in space and time.
234 Energy is often termed the currency of life, and animals are expected to use habitats and display
235 movement paths that optimize energy acquisition with direct links to fitness. Yet, if an animal
236 encounters a predator, it may be killed, rendering future (and possibly lifetime depending on the
237 individual circumstances such as life-stage or age or reproductive strategy) fitness zero. Clearly,
238 the concepts of energy acquisition and use related to energy landscapes and potential interaction
239 with predators in the landscape of fear are interacting paradigms that complement each other and
240 collectively provide a more coherent understanding of mechanistic basis of spatial ecology and
241 decision-making within wild animals. The simple models presented here reveal how movement
242 pathways may be modulated by both energy and fear. Although there have been great strides
243 made in conceptualizing animal movement ecology [49], significant research gaps still exist [50].
244 We believe that the integration of the concepts of energy landscapes and landscapes of fear will
245 be a new frontier for understanding animal movement ecology which should help identify
246 important mechanisms modulating the spatial ecology of wild animals.

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254

255 **Figure 1. Energy and fear affect wild dog movement in space and time.** Wild dogs are often
256 killed by lions, and as a consequence, (A) wild dogs avoid areas that are heavily used by lions, in
257 many ecosystems. Data shown are utilization distributions from GPS collars in Liuwa Plains
258 National Park, Zambia. Data from 3,271 kilometers of directly observed hunting in the Selous
259 Game Reserve show that (B) wild dogs hunt 52% more often in areas that are little-used by lions,
260 (C) even though their rate of encounter with prey is decreased by 20% in such areas.

261

262 **Figure 2. Elk responses to wolf predation risk.** Responses to predation risk are likely to
263 intersect with energy landscapes in many ways, some overt and some subtle. In response to the
264 presence of wolves, elk become more vigilant and move out of open grasslands where they
265 prefer to forage, but are conspicuous. These strong responses are associated with much smaller
266 changes in elevation, slope, snow depth and speed of travel, suggesting that antipredator
267 responses are shaped by the energetic costs of locomotion and ‘cratering’ in snow for access to
268 grasses.

269 **Figure 3. Quantitative integration of paradigms.** Schematic diagram of two possible paths taken
270 by an animal ‘intending’ to move from A to B [the ‘intent’ is important here since the movement
271 destination and driver means that the end point is defined - A good example of such a scenario
272 would be a central place forager returning to the central place {nest/burrow etc.} at the end of a
273 foraging bout]. The squares denote the cost of transport (COT) for movement and are composed,
274 within the landscape, of low cost squares (‘L’ joules per metre – in grey) and high cost squares
275 (‘H’ Joules per metre – in red). Normally, if the COT were uniform across the landscape, the least
276 cost pathway between A and B would be a straight line (blue line in the Fig) and the total cost of
277 travel would be LD (where D = distance). In the case above, there is an area of higher COT so the

278 animal should follow the dashed black trajectory if $LD_1 < (LD_2 + HD_3)$ (where D_1 is the distance
279 covered by the black dashed line, D_2 is the distance covered by the blue line within the grey square
280 zone and D_3 is the distance covered by the blue line within the red square zone). If we insert a
281 predator area which the animal intends to avoid (the red ovoid), the extent of the deviation from
282 the minimum cost path, and specifically its cost, should give us some metric of the perceived
283 danger. This is given by the extra energy that the animal is prepared to spend to reach its goal
284 above the minimum cost. This energy can be summarized as; $Energy = (LD_4 + HD_5) - LD_1$ or
285 $Energy = (LD_4 + HD_5) - (LD_2 + HD_3)$, whichever is the lesser.

286

287 **Box 1. Seabirds balance energy and risk in the wild.** (A) Schematic diagram of a cross-section
288 of an urban seafront zone (adapted from Shepard et al. in press) showing how a prevailing
289 onshore wind hits the buildings and is forced up creating lift that varies as a function of distance
290 from the constructions. Herring gulls fly within this lift (e.g. black circle in diagram). Actual data
291 on lift and locality can be derived from computational fluid dynamic models – for example for
292 wind speeds of 5.5 m/s (presented in Shepard et al. [48]. Assuming that gliding gulls have a
293 power use of about 10 W [51] and have a glide polar (flight speed versus drop rate) as presented
294 in Shepard et al. (in press), the flight speed of gulls gliding at different distances from the
295 buildings can be calculated knowing that the birds maintain constant height (drop rate = lift rate).
296 (B) In turn, the gliding metabolic rate can be divided by the speed to derive the costs of transport
297 as a function of distance from the buildings). Herring gulls (circles in B) do not fly in the zone of
298 highest lift, which would give them the lowest travel costs, but prefer to occupy a more zone
299 distant where the probability of collision with the buildings is reduced.

300

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