



Swansea University  
Prifysgol Abertawe



## Cronfa - Swansea University Open Access Repository

---

This is an author produced version of a paper published in :  
*Trends in Ecology & Evolution*

Cronfa URL for this paper:  
<http://cronfa.swan.ac.uk/Record/cronfa31719>

---

### **Paper:**

Gallagher, A., Creel, S., Wilson, R. & Cooke, S. (2017). Energy Landscapes and the Landscape of Fear. *Trends in Ecology & Evolution*, 32(2), 88-96.  
<http://dx.doi.org/10.1016/j.tree.2016.10.010>

---

This article is brought to you by Swansea University. Any person downloading material is agreeing to abide by the terms of the repository licence. Authors are personally responsible for adhering to publisher restrictions or conditions. When uploading content they are required to comply with their publisher agreement and the SHERPA RoMEO database to judge whether or not it is copyright safe to add this version of the paper to this repository.  
<http://www.swansea.ac.uk/iss/researchsupport/cronfa-support/>

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

2 Austin J. Gallagher<sup>1,2,3\*</sup>, Scott Creel<sup>4</sup>, Rory P. Wilson<sup>5</sup>, Steven J. Cooke<sup>1</sup>

3 <sup>1</sup>Fish Ecology and Conservation Physiology Laboratory, Department of Biology and Institute of  
4 Environmental Science, Carleton University, Ottawa, ON K1S 5B6, Canada

5 <sup>2</sup>Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, FL 33149,  
6 USA

7 <sup>3</sup>Beneath the Waves, Inc., Miami, FL 33133, USA

8 <sup>4</sup>Department of Ecology, 310 Lewis Hall, Montana State University, Bozeman, MT 59717

9 <sup>5</sup>Biosciences, College of Science, Swansea University, Swansea SA2 8PP, UK

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

24

25

26

27

## 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),  $\epsilon$ , 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 ( $\epsilon$ ) 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  $\alpha$

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.

## 247 **Acknowledgements**

248 We thank our many colleagues for their thoughtful insights that greatly benefitted this article.  
249 Cooke is supported by the Natural Sciences and Engineering Research Council of Canada, Ocean  
250 Tracking Network Canada, and the Canada Research Chairs Program.

251  
252  
253  
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

301 **Literature Cited**

- 302 1 Nussbaum MC (1978) *Aristotle's De motu animalium: text with translation, commentary*  
303 *and interpretative essay*, Princeton University Press.
- 304 2 Laundré, J.W. *et al.* (2001) Wolves, elk, and bison: reestablishing the “landscape of fear”  
305 in Yellowstone National Park, U.S.A. *Can. J. Zool.* 79, 1401–1409
- 306 3 Stephens, D. *et al.* (2007) *Foraging: behavior and ecology.*, University of Chicago Press.
- 307 4 Shaw, A. and Kouzin, I. (2013) Migration or residency? The evolution of movement  
308 behavior and information usage in seasonal environments. *Am. Nat.* 181, 114–124
- 309 5 Davies, N. *et al.* (2012) *An Introduction to Behavioural Ecology*, John Wiley and Sons.
- 310 6 Charnov, E. (1976) Optimal foraging, the marginal value theorem. *Theor. Popul. Biol.* 9,  
311 129–136
- 312 7 Louzao, M. *et al.* (2014) Coupling instantaneous energy-budget models and behavioural  
313 mode analysis to estimate optimal foraging strategy: an example with wandering  
314 albatrosses. *Mov. Ecol.* 2, 8
- 315 8 Weibel, E.R. *et al.* (2004) Allometric scaling of maximal metabolic rate in mammals:  
316 Muscle aerobic capacity as determinant factor. *Respir. Physiol. Neurobiol.* 140, 115–132
- 317 9 Schmitz, O.J. *et al.* (2004) Trophic cascades: The primacy of trait-mediated indirect  
318 interactions. *Ecol. Lett.* 7, 153–163
- 319 10 Wilson, R.P. *et al.* (2012) Construction of energy landscapes can clarify the movement  
320 and distribution of foraging animals. *Proc. R. Soc. B Biol. Sci.* 279, 975–80
- 321 11 Shepard, E.L.C. *et al.* (2013) Energy landscapes shape animal movement ecology. *Am.*  
322 *Nat.* 182, 298–312
- 323 12 Creel, S. *et al.* (2009) Glucocorticoid stress hormones and the effect of predation risk on  
324 elk reproduction. *Proc. Natl. Acad. Sci. U. S. A.* 106, 12388–12393
- 325 13 Christianson, D. and Creel, S. (2010) A nutritionally mediated risk effect of wolves on  
326 elk. *Ecology* 91, 1184–1191
- 327 14 Brown, J.S. and Kotler, B.P. (2004) Hazardous duty pay and the foraging cost of  
328 predation. *Ecol. Lett.* 7, 999–1014
- 329 15 Bohrer, G. *et al.* (2012) Estimating updraft velocity components over large spatial scales:  
330 Contrasting migration strategies of golden eagles and turkey vultures. *Ecol. Lett.* 15, 96–  
331 103
- 332 16 Leichti, F. *et al.* (2000) Predicting migratory flight altitudes by physiological migration  
333 models. *Auk* 117, 205–214
- 334 17 Scantlebury, D.M. *et al.* (2014) Flexible energetics of cheetah hunting strategies provide  
335 resistance against kleptoparasitism. *Science* 346, 79–82
- 336 18 Dickinson, M.H. *et al.* (2000) How animals move: an integrative view. *Science* 288, 100–

- 337 106
- 338 19 Lejeune, T.M. *et al.* (1998) Mechanics and energetics of human locomotion on sand. *J.*  
339 *Exp. Biol.* 201, 2071–2080
- 340 20 White, W.T. and Yousef, M. (1978) Energy expenditure in reindeer walking on roads and  
341 on tundra. *Can. J. Zool.* 56, 215–223
- 342 21 Minetti, A.E. *et al.* (2002) Energy cost of walking and running at extreme uphill and  
343 downhill slopes. *J. Appl. Physiol.* 93, 1039–1046
- 344 22 Lima, S.L. and Dill, L.M. (1990) Behavioral decisions made under the risk of predation: a  
345 review and prospectus. *Can. J. Zool.* 68, 619–640
- 346 23 Estes, J.A. *et al.* (2011) Trophic downgrading of planet Earth. *Science* 333, 301–306
- 347 24 Laundre, J.W. *et al.* (2010) The Landscape of Fear: Ecological Implications of Being  
348 Afraid~!2009-09-09~!2009-11-16~!2010-02-02~! *Open Ecol. J.* 3, 1–7
- 349 25 Suraci, J.P. *et al.* (2016) Fear of large carnivores causes a trophic cascade. *Nat. Commun.*  
350 7, 10698
- 351 26 Ripple, W.J. and Beschta, R.L. (2003) Wolf reintroduction, predation risk, and  
352 cottonwood recovery in Yellowstone National Park. *For. Ecol. Manage.* 184, 299–313
- 353 27 Fortin, D. *et al.* (2005) Wolves influence elk movements: Behavior shapes a trophic  
354 cascade in Yellowstone National Park. *Ecology* 86, 1320–1330
- 355 28 Creel, S. *et al.* (2007) Predation Risk Affects Reproductive Physiology and Demography  
356 of Elk. *Science* 315, 960
- 357 29 Winnie, J.A. (2012) Predation risk, elk, and aspen: tests of a behaviorally mediated trophic  
358 cascade in the Greater Yellowstone Ecosystem. *Ecology* 93, 2600–2614
- 359 30 Hebblewhite, M. and Merrill, E. (2009) Trade-offs between predation risk and forage  
360 differ between migrant strategies in a migratory ungulate. *Ecology* 90, 3445–3454
- 361 31 Werner, E.E. *et al.* (2015) An Experimental Test of the Effects of Predation Risk on  
362 Habitat Use in Fish. 64, 1540–1548
- 363 32 Creel, S. and Creel, N. (1995) Communal hunting and pack size in African wild dogs,  
364 *Lycaon pictus*. *Anim. Behav.* 50, 1325–1339
- 365 33 Estes, R. and Goddard, J. (1967) Prey selection and hunting behavior of the African wild  
366 dog. *J. Wildl. Manage.* 1, 52–70
- 367 34 Hayward O’Brien, J., Hofmeyr, M., Kerley, G.I.H., M.W. *et al.* (2006) Prey preferences  
368 of the African wild dog *Lycaon pictus*: ecological requirements for their conservation. *J.*  
369 *Mammal.* 87, 1122–1131
- 370 35 Creel, S. and Creel, N. (1996) Limitation of African Wild Dogs by Competition  
371 Limitation with Larger Carnivores. *Conserv. Biol.* 10, 526–538
- 372 36 Mills, M. and Gorman, M. (1997) Factors affecting the density and distribution of wild



373 dogs in the Kruger National Park. *Conserv. Biol.* 11, 1397–1406

374 37 Owen-Smith, N. and Mills, M.G.L. (2008) Predator-prey size relationships in an African  
375 large-mammal food web. *J. Anim. Ecol.* 77, 173–183

376 38 Gorman, M.L. *et al.* (1998) High hunting costs make African wild dogs vulnerable to  
377 kleptoparasitism by hyaenas. *Nature* 392, 1992–1994

378 39 Fanshawe, J. and Fitzgibbon, C. (1993) Factors influencing the hunting success of an  
379 African wild dog pack. *Anim. Behav.* 45, 479–490

380 40 Creel, S. *et al.* (2001) Interspecific competition & population biology of extinction-prone  
381 carnivores. In *Carnivore Conservation* (Gittleman, J. *et al.*, eds), pp. 35–61, Cambridge

382 41 Creel, S. (1997) Cooperative hunting and group size: assumptions and currencies. *Anim.*  
383 *Behav.* 54, 1319–24

384 42 Creel, S. and NM, C. (2002) *The African Wild Dog: Behavior, Ecology and Conservation*,  
385 Princeton University Press.

386 43 Woodroffe, R. *et al.* (2007) Rates and causes of mortality in Endangered African wild  
387 dogs *Lycaon pictus*: lessons for management and monitoring. *Oryx* 41, 215–233

388 44 Swanson, A. *et al.* (2014) Cheetahs and wild dogs show contrasting patterns of  
389 suppression by lions. *J. Anim. Ecol.* 83, 1418–1427

390 45 Wilson, R. *et al.* (2013) Turn costs change the value of animal search paths. *Ecol. Lett.* 16,  
391 1145–1150

392 46 Creel, S. *et al.* (2005) Elk alter habitat selection as an antipredator response to wolves.  
393 *Ecology* 86, 3387–3397

394 47 Winnie, J.A. *et al.* (2006) Elk decision-making rules are simplified in the presence of  
395 wolves. *Behav. Ecol. Sociobiol.* 61, 277–298

396 48 Shepard, Emily L C, Williamson, C. and Windsor, S.P. Fine-scale flight strategies of gulls  
397 in urban airflows indicate risk and reward in city living. *Philos. Trans. R. Soc. Lond. B.*  
398 *Biol. Sci.*

399 49 Holyoak, M. *et al.* (2008) Movement Research. *Proc. Natl. Acad. Sci.* 105, 19052–19059

400 50 Holyoak, M. *et al.* (2008) Trends and missing parts in the study of movement ecology.  
401 *Proc. Natl. Acad. Sci. U. S. A.* 105, 19060–19065

402 51 Baudinette, R. and Schmidt-Nielsen, K. (1974) Energy cost of gliding flight in herring  
403 gulls. *Nature* 248, 83–84

404