Energy Landscapes and the Landscape of Fear — **Source link**

Austin J. Gallagher, Austin J. Gallagher, Scott Creel, Rory P. Wilson ...+1 more authors

Institutions: Carleton University, University of Miami, Montana State University, Swansea University

Published on: 01 Feb 2017 - Trends in Ecology and Evolution (Trends Ecol Evol)

Topics: Animal ecology, Ecology (disciplines) and Spatial ecology

Related papers:

- A movement ecology paradigm for unifying organismal movement research

- Behavioral decisions made under the risk of predation: a review and prospectus

- The Landscape of Fear: Ecological Implications of Being Afraid~!2009-09-09~!2009-11-16~!2010-02-02~!

- The Landscape of Fear: Ecological Implications of Being Afraid

- Energy Landscapes Shape Animal Movement Ecology

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

_____

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

2   Austin J. Gallagher[1,2,3*], Scott Creel[4], Rory P. Wilson[5], Steven J. Cooke[1]

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

5   [2]Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, FL 33149,
6   USA

7   [3]Beneath the Waves, Inc., Miami, FL 33133, USA

8   [4]Department of Ecology, 310 Lewis Hall, Montana State University, Bozeman, MT 59717

9   [5]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

24

25

26

27

The mechanistic basis of animal movement

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

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

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

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    $$EE = \int P \, dt \tag{1}$$

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   $$P = RMR + f(\varepsilon) \tag{2}$$

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   $$EE_{min} = argmin_p \left[\int_{t0}^{tn} RMR + f(\varepsilon) dt \right] \tag{3}$$

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 *a*

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 life. 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

Conclusion

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.

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

Literature Cited

301

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 m igrant 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* 852, 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