CellPress

Opinion
Energy Landscapes and the Landscape of Fear

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

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

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 stimulated the study of animal ecology dating back to questions posed by Aristotle nearly 2300 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' that have since been applied to studies in the wild [3], changing the way the biological community thought about animal movement and prey selection [6].

However, this approach, while 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 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 involve significant energy expenditure by animals [8,9] and it is now clear that the risk of predation can also structure how animals use their landscapes [2,10].

Trends

Animals are not distributed randomly in space and time because their movement ecology is influenced by a variety of factors.

Energy landscapes and the landscape of fear have recently emerged as largely independent paradigms, both reshaping our perspectives and thinking relating to the spatial ecology of animals across heterogeneous landscapes.

We argue that the fear and energy paradigms are complementary and collectively provide a better mechanistic basis for understanding the spatial ecology and decision-making of wild animals.

A quantitative framework for merging these ideas in wild animals is presented.

[1]Fish Ecology and Conservation Physiology Laboratory, Department of Biology and Institute of Environmental Science, Carleton University, Ottawa, ON K1S 5B6, Canada
[2]Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, FL 33149, USA
[3]Beneath the Waves, Inc., Miami, FL 33133, USA
[4]Department of Ecology, 310 Lewis Hall, Montana State University, Bozeman, MT 59717, USA
[5]Biosciences, College of Science, Swansea University, Swansea SA2 8PP, UK

*Correspondence:
agallagher@rsmas.miami.edu
(A.J. Gallagher).

CrossMark

The fact that important attributes of landscapes vary in both space and time has been the central tenet of two separate and divergent research themes, both of which are now receiving increasing attention in the research communities studying wild animal biology and ecology; energy landscapes, and the landscape of fear [2,9]. In the case of energy landscapes, it is the variable cost of transport associated with animal locality (and time) that influences animal movement [9,11]. The landscape of fear, by contrast, is grounded in the controlling effects predators can have on prey, which trigger food versus risk trade-offs that can change animal behavior including movement [12,13]. Theory and methodological innovation are at the core of both research themes. While they are both believed to have great power in the ability to predict animal movement, they seem to be moving independently in different directions although they should be integrated together to represent the real world. Here we propose to merge concepts central to energy landscapes with those relevant to the landscape of fear to provide a framework that enhances our ability to understand how animals are distributed in space and time. We briefly discuss the theoretical, biological, and ecological underpinnings of both research themes and illustrate the justification for their integration through two real-world ecological examples. We then explore this idea quantitatively by constructing models of movement pathways modulated by energy and fear in the hope that our framework can be used to calculate the amount of extra energy an animal is willing to spend to avoid predators (i.e., the cost of predation risk and danger) based on animal movement data. We hope that this framework will demonstrate potential for better understanding of why animals move and how they are distributed in space and time.

Energy Landscapes

The costs of movement often depend on the environment through which an animal moves. Remarkably, although studies examining animal movement during migration have emphasized the importance of barriers and flow streams (in air and water) in modulating movement [14,15], few have demonstrated the role that these variable energy costs play in animal space use and movement on a day-to-day basis [14,16]. Dickenson *et al.* [17] note that determinations of the costs of locomotion in a laboratory setting are unlikely to be applicable to the wild. Unsurprisingly, therefore, where authors have examined how natural environments affect the cost of locomotion, the variation in energy expenditure with environment type is indeed impressive. For example, we know that humans walking on 'soft sand' require 2.1–2.7 times more energy than on solid rock [18,19] and that people walking up slopes experience an increase in cost of transport with slope angle, such that a man walking up a 45° slope expends 17 times more energy per meter than when walking on the flat [20].

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

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

$$EE = \int P dt \qquad [1]$$

where P = power. More properly, however, power use would also be a function of the energy landscape ε, so that:

$$P = RMR + f(\varepsilon) \qquad [2]$$

If, other things being equal, animals attempted to minimize traveling costs between two points, we would expect them to display a trajectory where the sum costs of all speeds and turns of the

chosen trajectory across the different energy landscapes were minimized (EE_{min}), so that:

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

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

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

The Landscape of Fear

In its initial representation, the 'landscape of fear' was based on predators eliciting, in their prey, a fear of being killed (the risk of predation) throughout the ecosystem [2]. These 'fear effects' can significantly alter the physiology, behavior, and life history of prey species [21]. This 'ecology of fear' is increasingly being recognized as crucial in understanding the role of predators, the mechanics of predator–prey interactions, and even the ecosystem-wide consequences of removing predators from natural systems [22]. It has been proposed that the spatial and temporal manner in which wild animals utilize their landscapes is fear driven and that it permeates all areas of ecology [23]. This natural game of cat and mouse between predators and their prey affects how both groups navigate their landscapes. This landscape of fear interaction, which integrates concepts from psychology, ecology, and geology [2], is thought to drive direct changes in prey distribution and, consequently, indirect changes in lower trophic level resources. Thus, the landscape of fear acts as a buffer to lower trophic levels from overconsumption by other consumers (usually herbivores) and has been linked to the occurrence of trophic cascades [24]. A well-known (but still controversial) example of this concept is the reintroduction of wolves in Yellowstone National Park, whereby the reinsertion of the fear of mortality due to wolves has been correlated with changes in elk reproductive fitness, decreases in elk populations, and changes in the structure of the natural landscapes [12,25–28].

Predator ecologists have suggested that failing to consider the landscape of fear will underestimate the effect that large carnivores play. While this concept is well established in the ecological community, the costs of the risk of predation are rarely quantified beyond food–risk, mesocosm-based approaches [29] or correlations and are instead an inferred construct of the effects of predation risk on prey.

We suggest that the landscape of fear should also be expanded beyond a simple visual model of predation risk to include movement as the driver of animal distribution in space and time. Any space-linked process that may lead to death may be couched in terms of space- or landscape-linked 'fear'. Examples are environmentally challenging terrains, such as cliffs for ungulates or downdraughts for birds, whose value may also change over time and there is no reason why such phenomena cannot be treated within the same framework. Thus, while we know that the risk of being killed in a general sense can affect animal movements, our understanding of how it changes their distribution in space and time is lacking [30].

Consequently, the landscape of fear remains vaguely described, particularly regarding other components, as species navigate their landscapes. Integrating separate yet complementary concepts surrounding animal decision-making should provide a more holistic understanding of how energy and fear drive the distribution of free-ranging animals. Here we present tractable

real-world case studies that demonstrate the integration of energy landscapes and the landscape of fear (i.e., the risk of being killed). We then provide a hypothetical example of quantifying them together to enhance our understanding of animal distribution.

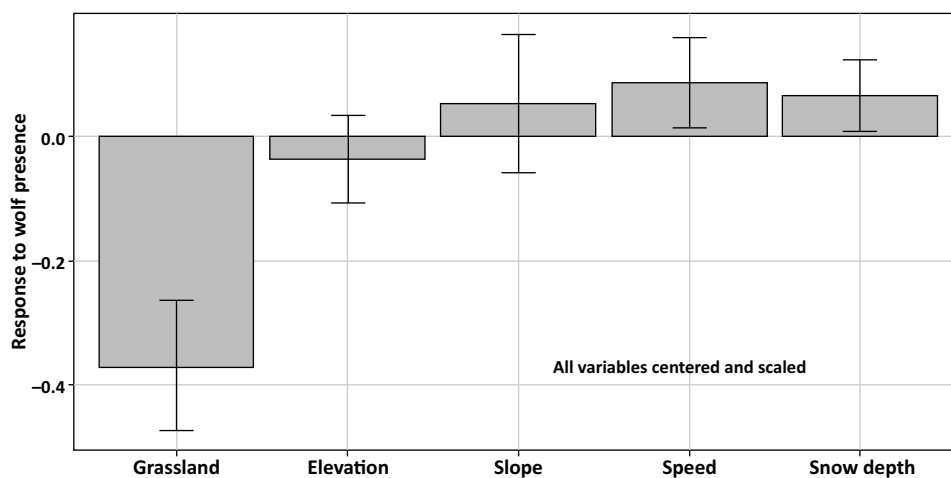## Case Study: African Wild Dogs

To illustrate intersections between predation risk and energetics with consequences for the distribution and abundance of a species, we note that the African wild dog (*Lycaon pictus*) commonly preys on species like wildebeest (*Connochaetes taurinus*), warthog (*Phacocoerus aethiopicus*), gazelles (*Gazella* spp.), and impala (*Aepyceros melampus*) that are also important prey for much larger carnivores including lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*) [31–33]. This dietary overlap creates the potential for interspecific competition [34–36], particularly given that the energetic costs of catching and killing ungulate prey are substantial [37], which creates an additional selection pressure favoring kleptoparasitism even if live prey are not in limited supply. Consequently, hyenas sometimes follow wild dogs while they are hunting (even before they make a kill) and where hyenas are abundant and visibility is good, hyenas displace wild dogs at up to 86% of their kills [34,38], although the rate of kleptoparasitism by hyenas varies 43-fold among published studies [39]. These food losses by wild dogs must be offset by increasing the energy invested in finding, catching, and killing prey, which is substantial even without losses to scavengers [37,40].
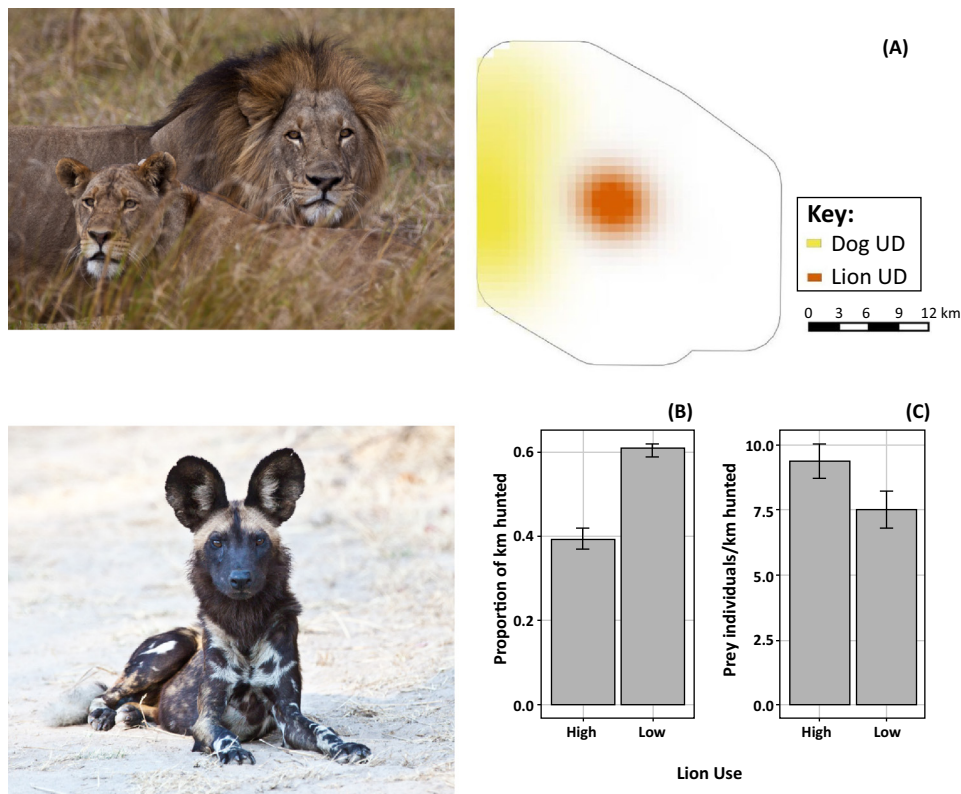
Figure 1. Energy and Fear Affect Wild Dog Movement in Space and Time. Wild dogs are often killed by lions and as a consequence (A) wild dogs avoid areas that are heavily used by lions in many ecosystems. Data shown are utilization distributions from GPS collars in Liuwa Plains National Park, Zambia. Data from 3271 km of directly observed hunting in the Selous Game Reserve show that (B) wild dogs hunt 52% more often in areas that are little used by lions, (C) although their rate of encounter with prey is decreased by 20% in such areas.

Importantly, however, the behavioral and morphological adaptations of large carnivores make the consequences of interference competition potentially severe, and conflict with lions is a common cause of death for wild dogs [35,41,42]. As a consequence wild dogs avoid lions at all spatiotemporal scales (Figure 1). At the finest scale, the most common response of wild dogs to an audio playback of lion roars is to stop, reverse direction, and quickly move several kilometers (unpublished data). At the scale of entire ecosystems, wild dog densities are low where lion (and hyena) densities are high [34,41]. At intermediate scales, wild dogs consistently avoid areas that are heavily used by lions [34,35,43]. In the Selous Game Reserve, avoidance of lions caused wild dogs to hunt most often in deciduous woodland, where their rates of encounter with prey (3.75 prey animals/km moved) were substantially lower than in habitats preferred by lions (mean = 9.88 prey animals/km moved). The changes in wild dog movement manifest through energetic mechanisms such as reduced rates of prey encounter, and there could be even more cryptic or subtle energetic costs. For example, changes in habitat structure may modulate the maximum speed of wild dogs in their pursuit of prey or the angles at which they can turn. Such subtle mechanisms, summed over several hunts per day and 365 days per year, may have appreciable effects on fitness, although this has not been quantified. Nevertheless, changes in decision-making related to wild dog distribution will be influenced by predation risk from lions


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

and hyenas as well as the costs of transport and this combined effect could be quantified as its own selective path of movement.

Field studies using GPS collars are beginning to address these more subtle interactions between risk and energy (Figure 2). For example, in a landscape with a mosaic of grassland and forest, the presence of wolves caused elk to shift from preferred foraging habitat in meadows to the protective cover of forests, but in a manner that produced relatively little change in elevation, slope or speed of travel [48]. This reveals that even strong habitat shifts in response to risk can be sensitive to the costs of movement. Even more subtly, foraging locations used by elk were strongly related to snow depth and density when wolves were absent, but not when wolves were present [49]. Because the costs of locomotion and digging for food depend on snow depth and condition, this represents an important interaction between the landscapes of energy and risk (Figure 2).
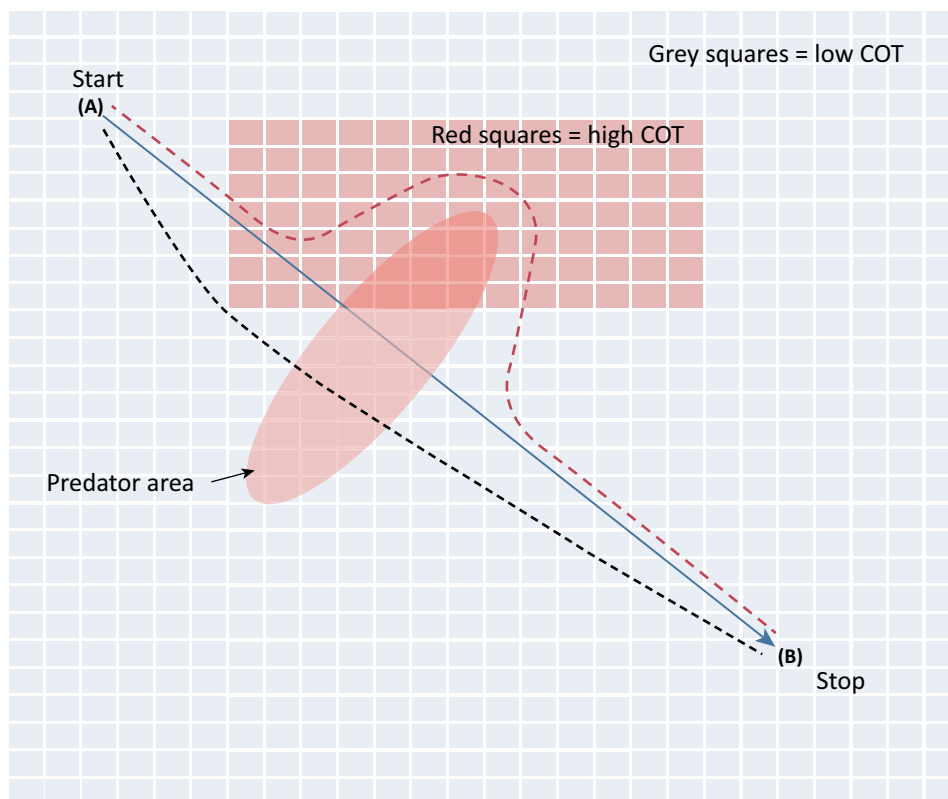
Trends in Ecology & Evolution

Figure 3. Quantitative Integration of Paradigms. Schematic diagram of two possible paths taken by an animal 'intending' to move from A to B [the 'intent' is important here, since the movement destination and driver means that the end point is defined – a good example of such a scenario would be a central-place forager returning to the central place (nest, burrow, etc.) at the end of a foraging bout]. The squares denote the cost of transport (COT) for movement and comprise, within the landscape, low-cost squares (L joules per meter, grey) and high-cost squares (H joules per meter, red). Normally, if the COT were uniform across the landscape the least-cost pathway between A and B would be a straight line (blue line in the figure) and the total cost of travel would be LD (where D = distance). In the case above, there is an area of higher COT so the animal should follow the broken black trajectory if $LD_1 < (LD_2 + HD_3)$ (where D_1 is the distance covered by the black broken line, D_2 is the distance covered by the blue line within the grey-square zone, and D_3 is the distance covered by the blue line within the red-square zone). If we insert a predator area that the animal intends to avoid (the red ovoid), the extent of the deviation from the minimum-cost path, and specifically its cost, should give us some metric of the perceived danger. This is given by the extra energy that the animal is prepared to spend to reach its goal above the minimum cost. This energy can be summarized as: Energy = $(LD_4 + HD_5) − LD_1$ or Energy = $(LD_4 + HD_5) − (LD_2 = HD_3)$, whichever is the lesser.

Case Study: Herring Gulls

Like all soaring birds, herring gulls (*Larus argentatus*) can accrue great energetic savings by selectively flying in areas with rising air, which allows them to glide rather than flap, so it is unsurprising that their medium-scale movement is partly modulated by the distribution of this lift. However, examining flight trajectories over a fine scale Shepard *et al.* [44] have shown that gulls using lift generated by onshore winds hitting seafront hotels do not position themselves in the position of highest lift, which is immediately adjacent to the buildings (Figure 2). Instead, they fly 10–20 m away, where the collision risk is reduced. Data presented in the work by Shepard *et al.* [44] allow some simple calculations to see the extent to which the risk is traded for energy (Box 1),

---

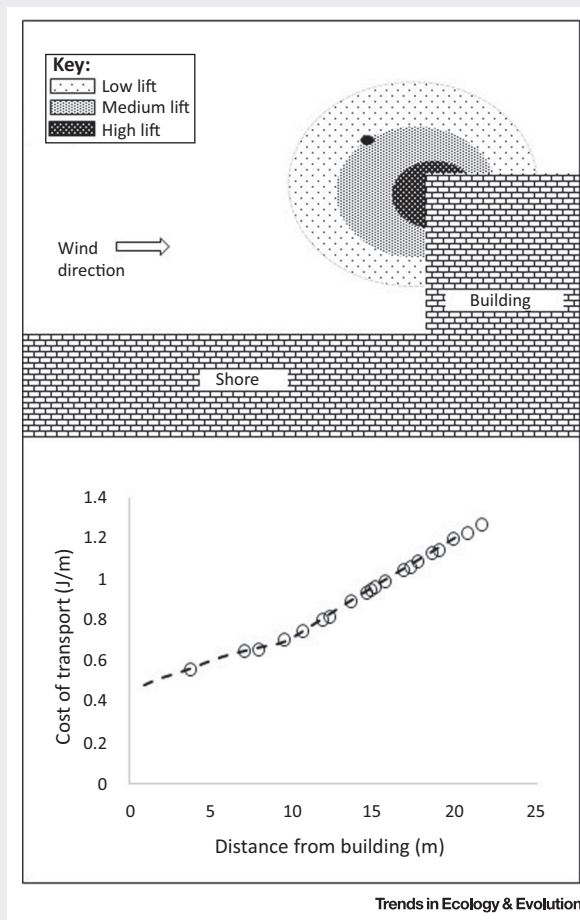**Box 1. Herring gulls balance energy and risk when flying.**

Figure I.

Figure I. Seabirds Balance Energy and Risk in the Wild. (A) Schematic diagram of a cross-section of an urban seafront zone (adapted from E.L.C. Shepard *et al.*, [44]) showing how a prevailing onshore wind hits the buildings and is forced upwards, creating lift that varies as a function of distance from the constructions. Herring gulls fly within this lift (e.g., black circle in diagram). Actual data on lift and locality can be derived from computational fluid dynamics models; for example, for wind speeds of 5.5 m/s (presented in [44]). Assuming that gliding gulls have a power use of about 10 W [47] and have a glide polar (flight speed versus drop rate) as presented in E.L.C. Shepard *et al.* [44], the flight speed of gulls gliding at different distances from the buildings can be calculated knowing that the birds maintain constant height (drop rate = lift rate). (B) In turn, the gliding metabolic rate can be divided by the speed to derive the cost of transport as a function of distance from the buildings. Herring gulls (circles in B) do not fly in the zone of highest lift, which would give them the lowest travel cost, but prefer to occupy a more distant zone where the probability of collision with the buildings is reduced.

so that energy losses can be equated directly with distances to life-threatening features within the environment.

Integrating Concepts

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

Concluding Remarks

Animal ecology has become increasingly mechanistic in recent years, with researchers applying various paradigms to understand how animals are distributed in space and time. Energy is often termed the currency of life and animals are expected to use habitats and display movement paths that optimize energy acquisition with direct links to fitness. However, if an animal encounters a predator it may be killed, rendering future (and possibly lifetime, depending on individual circumstances such as life stage or age) fitness zero. The concepts of energy acquisition and use related to energy landscapes and potential interaction with predators in the landscape of fear are interacting paradigms that complement each other and collectively provide new insights into the mechanistic basis of spatial ecology and decision-making within wild animals. The simple models presented here reveal how movement pathways may be modulated by both energy and fear. Although great strides have been made in conceptualizing animal movement ecology [45], significant research gaps remain [46]. We believe that the integration of the concepts of energy landscapes and landscapes of fear offers an exciting new perspective for understanding animal movements and gives researchers the potential to scale innovation within their own research, ranging from controlled laboratory experiments to studies tracking the migrations of Earth's largest species (see Outstanding Questions).

Outstanding Questions

Is it possible to integrate energetic and risk (i.e., fear) data through animal-borne tagging methodologies?

What are the conservation applications for integrating these paradigms?

Might this merging work be better for predators or prey?

References

1. Nussbaum, M.C. (1978) *Aristotle's De Motu Animalium: Text with Translation, Commentary and Interpretative Essay,* Princeton University Press
2. Laundré, J.W. *et al.* (2001) Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, U.S.A. *Can. J. Zool.* 79, 1401–1409
3. Stephens, D. *et al.* (2007) *Foraging: Behavior and Ecology,* University of Chicago Press
4. Shaw, A. and Kouzin, I. (2013) Migration or residency? The evolution of movement behavior and information usage in seasonal environments. *Am. Nat.* 181, 114–124
5. Davies, N. *et al.* (2012) *An Introduction to Behavioural Ecology,* John Wiley & Sons
6. Charnov, E. (1976) Optimal foraging, the marginal value theorem. *Theor. Popul. Biol.* 9, 129–136
7. Louzao, M. *et al.* (2014) Coupling instantaneous energy-budget models and behavioural mode analysis to estimate optimal foraging strategy: an example with wandering albatrosses. *Mov. Ecol.* 2, 8
8. Weibel, E.R. *et al.* (2004) Allometric scaling of maximal metabolic rate in mammals: muscle aerobic capacity as determinant factor. *Respir. Physiol. Neurobiol.* 140, 115–132
9. Wilson, R.P. *et al.* (2012) Construction of energy landscapes can clarify the movement and distribution of foraging animals. *Proc. Biol. Sci.* 279, 975–980
10. Schmitz, O.J. *et al.* (2004) Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecol. Lett.* 7, 153–163
11. Shepard, E.L.C. *et al.* (2013) Energy landscapes shape animal movement ecology. *Am. Nat.* 182, 298–312
12. Creel, S. *et al.* (2009) Glucocorticoid stress hormones and the effect of predation risk on elk reproduction. *Proc. Natl. Acad. Sci. U.S.A.* 106, 12388–12393
13. Christianson, D. and Creel, S. (2010) A nutritionally mediated risk effect of wolves on elk. *Ecology* 91, 1184–1191
14. Bohrer, G. *et al.* (2012) Estimating updraft velocity components over large spatial scales: contrasting migration strategies of golden eagles and turkey vultures. *Ecol. Lett.* 15, 96–103
15. Leichti, F. *et al.* (2000) Predicting migratory flight altitudes by physiological migration models. *Auk* 117, 205–214
16. Scantlebury, D.M. *et al.* (2014) Flexible energetics of cheetah hunting strategies provide resistance against kleptoparasitism. *Science* 346, 79–82
17. Dickinson, M.H. *et al.* (2000) How animals move: an integrative view. *Science* 288, 100–106
18. Lejeune, T.M. *et al.* (1998) Mechanics and energetics of human locomotion on sand. *J. Exp. Biol.* 201, 2071–2080
19. White, R.G. and Yousef, M.K. (1978) Energy expenditure in reindeer walking on roads and on tundra. *Can. J. Zool.* 56, 215–223

20. Minetti, A.E. *et al.* (2002) Energy cost of walking and running at extreme uphill and downhill slopes. *J. Appl. Physiol.* 93, 1039–1046

21. Lima, S.L. and Dill, L.M. (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* 68, 619–640

22. Estes, J.A. *et al.* (2011) Trophic downgrading of planet Earth. *Science* 333, 301–306

23. Laundre, J.W. *et al.* (2010) The landscape of fear: ecological implications of being afraid. *Open Ecol. J.* 3, 1–7

24. Suraci, J.P. *et al.* (2016) Fear of large carnivores causes a trophic cascade. *Nat. Commun.* 7, 10698

25. Ripple, W.J. and Beschta, R.L. (2003) Wolf reintroduction, predation risk, and cottonwood recovery in Yellowstone National Park. *For. Ecol. Manag.* 184, 299–313

26. Fortin, D. *et al.* (2005) Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology* 86, 1320–1330

27. Creel, S. *et al.* (2007) Predation risk affects reproductive physiology and demography of elk. *Science* 315, 960

28. Winnie, J.A., Jr (2012) Predation risk, elk, and aspen: tests of a behaviorally mediated trophic cascade in the Greater Yellowstone Ecosystem. *Ecology* 93, 2600–2614

29. Brown, J.S. and Kotler, B.P. (2004) Hazardous duty pay and the foraging cost of predation. *Ecol. Lett.* 7, 999–1014

30. Hebblewhite, M. and Merrill, E.H. (2009) Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. *Ecology* 90, 3445–3454

31. Creel, S. and Creel, N. (1995) Communal hunting and pack size in African wild dogs, *Lycaon pictus*. *Anim. Behav.* 50, 1325–1339

32. Estes, R. and Goddard, J. (1967) Prey selection and hunting behavior of the African wild dog. *J. Wildl. Manag.* 31, 52

33. Hayward O'Brien, J. *et al.* (2006) Prey preferences of the African wild dog *Lycaon pictus*: ecological requirements for their conservation. *J. Mammal.* 87, 1122–1131

34. Creel, S. and Creel, N.M. (1996) Limitation of African wild dogs by competition limitation with larger carnivores. *Conserv. Biol.* 10, 526–538

35. Mills, M.G. and Gorman, M.L. (1997) Factors affecting the density and distribution of wild dogs in the Kruger National Park. *Conserv. Biol.* 11, 1397–1406

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

37. Gorman, M.L. *et al.* (1998) High hunting costs make African wild dogs vulnerable to kleptoparasitism by hyaenas. *Nature* 852, 1992–1994

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

39. Creel, S. *et al.* (2001) Interspecific competition and population biology of extinction-prone carnivores. In *Carnivore Conservation* (Gittleman, J. *et al.*, eds), pp. 35–61, Cambridge University Press

40. Creel, S. (1997) Cooperative hunting and group size: assumptions and currencies. *Anim. Behav.* 54, 1319–1324

41. Creel, S. and Creel, N.M. (2002) *The African Wild Dog: Behavior, Ecology and Conservation,* Princeton University Press

42. Woodroffe, R. *et al.* (2007) Rates and causes of mortality in endangered African wild dogs *Lycaon pictus*: lessons for management and monitoring. *Oryx* 41, 215

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

44. Shepard, E.L.C. *et al.* (2016) Fine-scale flight strategies of gulls in urban airflows indicate risk and reward in city living. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* Published online September 26, 2016. http://dx.doi.org/10.1098/rstb.2015.0394

45. Holyoak, M. *et al.* (2008) Movement research. *Proc. Natl. Acad. Sci. U.S.A.* 105, 19052–19059

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

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

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

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