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Energy landscapes and the landscape of fear

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Abstract

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 re-shaping our perspectives and thinking about 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 the complementary nature through case studies, then integrate these concepts quantitatively by constructing models of movement pathways modulated by energy and fear to elucidate the mechanisms underlying the spatial ecology of wild animals.

Keywords: animal ecology; energy, fear, predators, movement
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
expenditures of animals [8][10], and it is now clear that the risk of predation can also structure how animals use their landscapes [2,9].

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 today receiving increasing attention in the research communities studying wild animal biology and ecology; energy landscapes and the landscape of fear [2,10]. With respect to energy landscapes, recent work has highlighted that the characteristics of the environment through which an animal moves, irrespective of whether it is water, air or over ground, profoundly affect the power use of the moving animal and therefore the costs of movement per meter travelled (the costs of transport) [10,11]. The landscape of fear, on the other hand, is grounded in the controlling effects predators can have on prey, which trigger food vs. risk trade-offs which can change animal behavior including movement [12,13]. Theory and methodological innovation (e.g., biotelemetry and biologging) are at the core of both research themes. While they are both believed to have great power in the ability to predict animal movement, each seems 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 operationalize this idea by constructing models of movement pathways modulated by energy and fear in hopes 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) [14] 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 depend on the environment through which an animal moves. Although studies examining animal movement during migration have emphasized the importance of barriers and flow streams (in air and water) in modulating movement [15,16], few have demonstrated the role that these variable energy costs play in animal space use and movement on a day to day basis [15,17]. Indeed, Dickenson et al. [18] 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 impressive. For example, we know that humans walking on ‘soft sand’ require 2.1-2.7 times more energy than on solid rock [19,20] 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 metre than walking on the flat [21]. Similarly, a bird flying into a wind at the speed of the wind has infinite travel costs while if that same bird flies with the wind, it will have transport costs it would have in still air.

So, given the ability to allude to the interaction between space, movement, energy expenditure and behaviour 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 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:

$$EE = \int P \, dt$$

Where $P = \text{power}$. More properly though, power use would also be a function of the energy landscape and routine metabolic rate (RMR), $\varepsilon$, so that

$$P = RMR + f(\varepsilon)$$

If, other things being equal, animals attempted to minimize travelling 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;

$$EE_{min} = \arg\min_P \left[ \int_{t_0}^{t_n} RMR + f(\varepsilon) \, dt \right]$$

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 ($\varepsilon$) 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 only one element though – 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 [22].
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 [23]. 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 animal ecology [24]. 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, neuroscience, ecology, and biogeography [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 over-consumption by other consumers (usually herbivores), and it has been linked to the occurrence of trophic cascades [25]. A well-known example of this concept is the reintroduction of wolves in Yellowstone National Park, whereby the re-insertion of the fear of mortality by wolves has been correlated with changes in elk reproductive fitness, decreases in elk populations, and dramatic changes in the structure of the natural landscapes [12,26–29].

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 [14] or correlations, and they tend to be an inferred construct of the effects of predation risk on prey.

Beyond this though, we suggest that the landscape of fear should also be expanded beyond the risk of being predated to any space-linked process that may lead to death in a probabilistic sense. Examples include environmentally challenging terrains, such as cliffs for ungulates, or downdraughts for birds, whose value may also change over time, and there is no a
priori reason why such phenomena should not be treated within the same framework.

Nevertheless, we concentrate our discourse on ‘fear’ being used to describe the fear of being killed because, while we know that the risk of being killed in a general sense can affect animal movements (particularly large vertebrates), our understanding of how it actually changes their distribution in space and time is lacking [30,31].

Given the above, the landscape of fear remains rather vaguely described, particularly as it related to how 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 a series of real-world, well-studied examples that empirically demonstrate the integration of both energy landscapes and the landscape of fear (i.e., the risk of being killed). We then provide a hypothetical example for quantifying them together to enhance our understanding of animal distribution.

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

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

To illustrate intersections between risk and energetics with consequences for the distribution and abundance of a species, consider the African wild dog (*Lycaon pictus*). Wild
dogs commonly prey on species like wildebeest (*Connochaetes taurinus*), warthog (*Phacocoerus africanus*), gazelles (*Gazella* spp.) and impala (*Aepyceros melampus*) that are important prey for much larger carnivores including lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*) (*Crocuta crocuta*) [32–34], and this dietary overlap creates the potential for interspecific competition [35–37]. The energetic costs of catching and killing ungulate prey are substantial [38], 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 [35,39], although the rate of kleptoparasitism by hyenas varies 43-fold among published studies [40]). 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 [38,41]

Moreover, 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 [36,42,43]. As a consequence, wild dogs avoid lions at all spatio-temporal scales (Fig. 1). At the finest scale, the most common response of wild dogs to nearby lion roars is to stop, reverse direction and rapidly move several kilometers away. At the scale of entire ecosystems, wild dog densities are low where lion (and hyena) densities are high [35,42]. At intermediate scales, wild dogs consistently avoid areas that are heavily used by lions (Fig.1) [35,36,44] and in the Selous Game Reserve, this avoidance of lions has caused wild dogs to hunt most often in deciduous woodland, where their rates of encounter with prey (3.8 prey animals/km moved) are substantially lower than in habitats preferred by lions (9.9 prey animals/km moved) (Fig. 1).
But these data only show that lions and spotted hyenas limit wild dogs in large part by energetic mechanisms such as food loss, reduced rates of prey encounter, forced changes in travel routes and rapid avoidance movements. We speculate that movement-related energetic consequences of risk avoidance are highly likely to exist beyond this, not least because the environment is different, affecting power costs for movement in a more subtle manner. For example, prey pursuit of prey by wild dogs in deciduous woodland will necessarily involve a more tortuous path than on the open grasslands, with correspondingly increased power use due to the substantial energetic costs of turning [45]. Such effects, summed over several hunts per day and 365 days per year, could have appreciable effects on fitness.

Field studies using GPS collars are beginning to quantify these more subtle interactions between risk and energy (Fig. 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 [46]. 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 [47]. 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 (Fig. 2).

To summarize, the costs of antipredator responses are often strongly tied to energetics. A better understanding of this intersection will require simultaneous attention to measurements of risk, foraging success [14] and energy expenditure.
Box 1. Fear and energy landscapes integrated in mid-air: Herring gulls

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

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 to 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 the landscape of fear, or indeed any other constraint (Fig. 3).
Conclusion

Animal ecology has become increasingly mechanistic in recent years, with researchers applying different 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. Yet, if an animal encounters a predator, it may be killed, rendering future (and possibly lifetime depending on the individual circumstances such as life-stage or age or reproductive strategy) fitness zero. Clearly, 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 a more coherent understanding of 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 there have been great strides made in conceptualizing animal movement ecology [49], significant research gaps still exist [50]. We believe that the integration of the concepts of energy landscapes and landscapes of fear will be a new frontier for understanding animal movement ecology which should help identify important mechanisms modulating the spatial ecology of wild animals.

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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 3,271 kilometers 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) even though their rate of encounter with prey is decreased by 20% in such areas.

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.

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 are composed, within the landscape, of low cost squares (‘L’ joules per metre – in grey) and high cost squares (‘H’ Joules per metre – in 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 Fig) 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 dashed black trajectory if $L_D^1 < (L_D^2 + H_D^3)$ (where $D_1$ is the distance covered by the black dashed 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 which 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; $\text{Energy} = (L_D^4 + H_D^5) - L_D^1$ or $\text{Energy} = (L_D^4 + H_D^5) - (L_D^2 = H_D^3)$, whichever is the lesser.

**Box 1. Seabirds balance energy and risk in the wild.** (A) Schematic diagram of a cross-section of an urban seafront zone (adapted from Shepard et al. in press) showing how a prevailing onshore wind hits the buildings and is forced up 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 dynamic models – for example for wind speeds of 5.5 m/s (presented in Shepard et al. [48]. Assuming that gliding gulls have a power use of about 10 W [51] and have a glide polar (flight speed versus drop rate) as presented in Shepard et al. (in press), 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 costs 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 costs, but prefer to occupy a more zone distant where the probability of collision with the buildings is reduced.
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