COMMENTARY

Terrestrial movement energetics: current knowledge and its application to the optimising animal

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ABSTRACT

The energetic cost of locomotion can be a substantial proportion of an animal's daily energy budget and thus key to its ecology. Studies on myriad species have added to our knowledge about the general cost of animal movement, including the effects of variations in the environment such as terrain angle. However, further such studies might provide diminishing returns on the development of a deeper understanding of how animals trade-off the cost of movement with other energy costs, and other ecological currencies such as time. Here, I propose the 'individual energy landscape' as an approach to conceptualising the choices facing the optimising animal. In this Commentary, first I outline previous broad findings about animal walking and running locomotion, focusing in particular on the use of net cost of transport as a metric of comparison between species, and then considering the effects of environmental perturbations and other extrinsic factors on movement costs. I then introduce and explore the idea that these factors combine with the behaviour of the animal in seeking short-term optimality to create that animal's individual energy landscape – the result of the geographical landscape and environmental factors combined with the animal's selected trade-offs. Considering an animal's locomotion energy expenditure within this context enables hard-won empirical data on transport costs to be applied to questions about how an animal can and does move through its environment to maximise its fitness, and the relative importance, or otherwise, of locomotion energy economy.

Introduction

Locomotion is a behaviour of fundamental importance, yet the energy that an animal expends while moving can significantly decrease the amount that it has available for growth and reproduction (Perrigo, 1987; Perrigo and Bronson, 1985; Zhao et al., 2013). An animal may also fatigue if it expends energy too quickly while moving, which could prove crucial, resulting in the failure to compete for or attract a mate (Lees et al., 2012), hunt down prey (Ydenberg and Clark, 1989) or elude a predator (Wilson et al., 2013a; Wirsing et al., 2002). Consequently, understanding the factors that influence the energetic cost of locomotion in animals has been and continues to be the subject of much research.

Since the late 1800s (Zuntz, 1897), researchers have been running humans and animals on treadmills and simultaneously measuring rates of respiratory gas exchange; this experimental design has been the mainstay of investigations into the energy costs of moving for a terrestrial animal. There are now data on the energetic cost of locomotion for over 200 species, encompassing disparate taxa of both ectotherms and endotherms, spanning the 1-mg fruit fly (Berrigan and Partridge, 1997) to the 3-tonne Asian elephant (Langman et al., 2012). More elaborate studies have quantified the moderating effects of a plethora of external factors on the costs of terrestrial locomotion, demonstrating the importance of the animal's environment in shaping its movement costs (e.g. Fancy and White, 1987; Lejeune et al., 1998). In this Commentary, I aim to bridge our past understanding of transport energy costs, largely considered from a physiological viewpoint, with current and future understanding around the implications of these costs for an animal's behaviour and fitness – an ecological perspective. First, I will introduce and discuss the fundamentally important concept of the net cost of transport for our understanding of the factors that govern the energetics of walking and running. Although previous studies have reviewed the literature about intrinsic influences on transport costs (body mass, morphology, biomechanics) (Full et al., 1990; Full, 1989; Rose et al., 2015), the ecological perspective provided in the present article shifts the focus to the effects of extrinsic influences (e.g. terrain). I will then ask how we might move beyond the descriptive to understand the implications of these environmental effects on the energy costs of walking. Interesting current research is exploring how the energy expenditure of movement helps drive an animal's ecology, i.e. how the costs of movement influence an animal's interactions with its environment (Scharf et al., 2016). I argue that we should couch the recently popularised notion of the energy landscape within the framework of the trade-offs made by an animal seeking to optimise its behaviour (i.e. to maximise its fitness). For example, an optimising animal might base its behaviours on trading off between reaching a food source quickly while moving cryptically. This approach to understanding the influence of an animal's movement costs on its ecology will allow us to conceptualise, and indeed quantify, those trade-off options.

Comparative energetics: the value of $NCOT_{min}$

An animal's energy expenditure is elevated when it walks, and movement costs can be a substantial part of an animal's daily energy budget (Garland, 1983; Gefen, 2011; Halsey et al., 2015; Nudds and Bryant, 2000; Rezende et al., 2009; Scantlebury et al., 2014; Speakman and Selman, 2003; Williams et al., 2014). Naturally then, there has been considerable interest in comparing the relative energy costs of different species. For most species, the rate at which energy is spent by an animal during locomotion is, to some good approximation, linearly correlated with the speed of their movement, at least on level ground (Fig. 1A) (Schmidt-Nielsen, 1972; Taylor et al., 1982, 1970; see also Hoyt and Taylor, 1981). The slope of the regression represents the minimum net cost of transport ($NCOT_{min}$): the cost per unit distance for an animal specifically to move itself. Thus the general linearity in the

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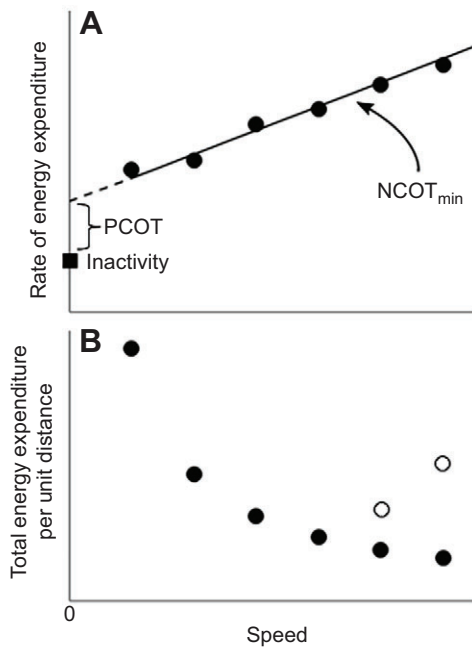*Author for correspondence (l.halsey@roehampton.ac.uk)

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Fig. 1. The hypothetical relationship between energy expenditure and the speed of locomotion. (A) The minimum net cost of transport ($NCOT_{min}$) is calculated as the linear slope of the relationship between the rate of energy expenditure and locomotion speed for speeds greater than zero. Extrapolation of the $NCOT_{min}$ line to $x=0$ indicates that during locomotion there are additional fixed energy costs represented by both the energetic costs for the animal that are not associated with activity ('inactivity') and an additional cost probably associated with the posture evoked during locomotion (postural cost; PCOT). (B) Consequently, although $NCOT_{min}$ is independent of locomotion speed, the total energy expended during locomotion over a given distance decreases with increasing speed because at higher speeds there is less time during which energy is spent on the fixed costs. These increasing efficiencies in energy expenditure as speed increases are attenuated at higher speeds because the fixed costs become a decreased proportion of total energy expenditure. It must be noted, however, that the fixed costs that would be paid even if the animal was inactive should not be considered an energy cost to locomote per se. Open circles show that total energy expenditure increases at higher speeds for species that exhibit a curvilinear $NCOT_{min}$.

Fig. 2. Larger animals tend to have higher absolute $NCOT_{min}$ and lower mass-specific $NCOT_{min}$. (A) The scaling of $\log_{10}$-transformed absolute $NCOT_{min}$ (ml m^{-1}) with $\log_{10}$-transformed body mass (kg) for 201 extant species spanning six orders of magnitude in size. (B) The scaling of $\log_{10}$-transformed mass-specific $NCOT_{min}$ (ml kg^{-1} m^{-1}) with $\log_{10}$-transformed body mass (kg) for the same species (filled circles). Open circles represent estimated values for dinosaurs based on power requirements modelled from measured hip heights (taken from Pontzer et al., 2009). The regression line is fitted to the extant data only [$\log(NCOT_{min})=-0.28\times\log(mass) -0.28$; phylogenetic least squares $r^2=0.85$].

relationship between rate of energy expenditure and speed, although not representing a mechanistic explanation, nonetheless makes basic comparisons of energy economy between disparate species remarkably straightforward.

Of course, larger animals tend to have a higher absolute $NCOT_{min}$ (Fig. 2A) (Taylor et al., 1970). Less obviously, they also tend to have a lower mass-specific $NCOT_{min}$ (Fig. 2B) (Cavagna and Legramandi, 2015; Full et al., 1990; Rose et al., 2015; Schmidt-Nielsen, 1972; Usherwood, 2013). We can infer from this relationship that, from the fly to the elephant, a key factor or factors well correlated with body size determine much of an animal's energy costs of locomotion. Indeed, relatively recent work has shown that the effective length of the limb is the primary anatomical driver of locomotor costs in terrestrial animals (Pontzer, 2007; Reilly et al., 2007). Interestingly, this appears to hold for dinosaurs as well; estimates of their power requirements to walk (modelled from measurements of hip height) fall consistently close to the line of best fit for extant species, across a great range of dinosaur body masses including the 6-tonne *Tyrannosaurus* (Fig. 2B) (Pontzer et al., 2009).

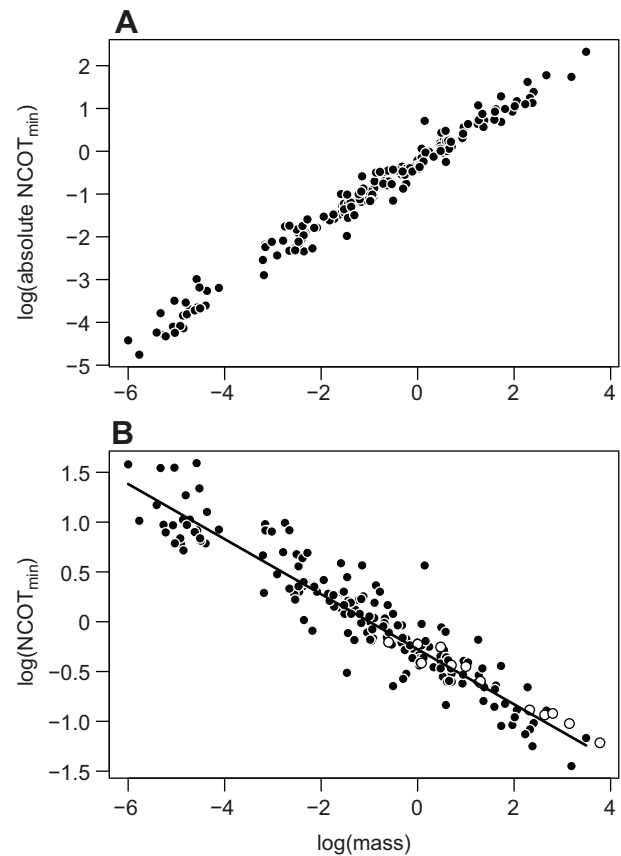However, although body mass statistically explains much of the variation in $NCOT_{min}$ between species, allometric plots are presented on log–log axes, which can hide the degree of variability in the data. In fact, species of a similar body size and shape can exhibit extraordinarily varied costs of transport; an animal's cost of locomotion for a particular distance travelled can be several-fold different to that of a similarly sized individual of a different species (Full et al., 1990). Part of this variation can be explained by the fact that measurements of rate of oxygen consumption at any given speed are imperfect, and linear fits of the data points to calculate $NCOT_{min}$ are also an approximation, adding further error. However, by no means can these caveats explain all the extraordinary variability identified by Full et al. (1990). Understanding the causes of these among-species differences in $NCOT_{min}$ beyond body size effects is important, because the energetic cost of locomotion influences a wide range of ecological patterns including space use (Wilson et al., 2011), dispersal (Niitepold et al., 2009) and activity patterns (Humphries and Careau, 2011).

However, even accounting for the relationship between body mass and $NCOT_{min}$, to date there are no reported robust differences in $NCOT_{min}$ between taxonomic groups that might indicate that certain morphological details, physiologies or evolutionary histories are associated with good or poor energy economies of walking (Full et al., 1990; Full and Tu, 1991). In other words, the $NCOT_{min}$ values

for all of the species within any given group straddle the linear line of best fit between $NCOT_{min}$ and mass across all measured species (Full et al., 1990).

The implications of speed-independent $NCOT_{min}$

The fact that $NCOT_{min}$ is approximately independent of speed in most animals studied implies that such animals expend the same amount of energy specifically to move themselves a given distance regardless of the speed at which they walk or run. From this we might infer that there is no energetic economy to be gained by an animal moving slowly or quickly. However, most animals appear to pay an energetic price simply for striking their locomotion posture; a fixed cost that is somewhat independent of speed, though has yet to be well explained (Fig. 1A) (see Halsey, 2013 for discussion). While moving, animals are also expending energy for bodily processes that are not associated with activity (Konarzewski and Książek, 2013); a further fixed cost. However, in contrast to the locomotion posture cost, this is one that would be paid anyway; thus, although it forms part of an animal's energy costs during movement, it cannot be counted as part of the energy forfeited specifically to undertake this behaviour. Despite these fixed costs, at higher velocities the inference that speed does not affect total energy costs during movement is reasonably accurate, because fixed energy costs become a minor concern; the total energy expended while moving from A to B varies little with locomotion speed. It is when the animal is travelling at the lower range of its speeds and thus the payment of the fixed costs is being made for longer that variation in velocity has a substantial effect on total energy expenditure during movement; when the animal speeds up slightly its energy economy per unit distance improves considerably. Conversely, when the animal slows down substantially, tending towards a speed of 0, the total energy cost for it to move between two points increases considerably (Fig. 1B).

Furthermore, for several species investigated so far, $NCOT_{min}$ does vary substantially with speed of locomotion. This variation presents either as a curvilinear relationship between rate of oxygen consumption and locomotion speed as seen for humans walking (Halsey and White, 2012) or, more subtly, when running (Steudel-Numbers and Wall-Scheffler, 2009), or as a shift in slope angle coinciding with a gait change (ground squirrels, Hoyt and Kenagy, 1988; mink, Williams, 1983). Where gait change is not the explanation, the fact that some species exhibit a more clearly curvilinear relationship than others may be due simply to the range of speeds over which those species have been measured. Animals are at risk of injury when they are run at high speeds, or they may fatigue or become anaerobic before reaching steady-state rates of oxygen consumption (Hoyt and Taylor, 1981; Taylor et al., 1971). Elephants and large ratite birds also show a non-linear relationship between rate of oxygen consumption and speed, and thus can select a speed that minimises $NCOT_{min}$ (Langman et al., 2012; Watson et al., 2011). This is also the case for horses, at least within some gaits (Hoyt and Taylor, 1981). Indeed, the locomotion speeds selected by animals both in laboratory experiments and in the wild are often similar to those representing the minimum total energy cost (Culik and Wilson, 1991; Hoyt and Taylor, 1981; Minetti et al., 2003; Wickler et al., 2000). Although this is yet to be tested, it is quite possible that some species showing a linear relationship between rate of oxygen consumption and speed on the treadmill would exhibit a non-linear relationship in other contexts, such as on a compliant substrate or moving into the wind (though this does not seem to be the case for incline running; Tullis and Andrus, 2011). At all locomotion speeds for these species, and at least at lower

locomotion speeds for species experiencing a more constant $NCOT_{min}$, the effect of speed on the total energetic cost of locomotion will play a role in determining the movement behaviour of an optimising animal.

Beyond treadmill NCOT
Environmental effects on locomotion costs

Empirical studies have revealed a plethora of variations in both environment and terrain that can affect the costs of an animal's movements. Although almost all findings to date are intuitive, they serve not only to confirm but also to quantify the effects of such variation on locomotion costs.

Humans walk at a greater energy cost on sand than on grass or firm ground (Lejeune et al., 1998; Pinnington and Dawson, 2001; White and Yousef, 1978), as the depth of snow increases (Pandolf et al., 1976), as depth of water increases (Halsey et al., 2014) and, more generally, as substrate stiffness decreases (Coward and Halsey, 2014; see also Kerdok et al., 2002). Increasing energy costs have also been recorded in reindeer walking in tundra as opposed to on a densely packed surface (White and Yousef, 1978) and in various quadruped mammals trudging deeper through snow (Crête and Larivière, 2003; Fancy and White, 1987). Such increased costs can be explained by the work done to deform the substrate (Coward and Halsey, 2014; Lejeune et al., 1998) and, in the case of snow, also to drag the limbs through it (Fancy and White, 1987). Considering the energy costs of these activities reveals the potential for terrestrial animals to save energy by moving as a group, though there has been little research into this; groups create paths as they progress through vegetation or over difficult substrates that may benefit individuals towards the rear.

An inclined terrain increases $NCOT_{min}$ owing to the work done against gravity, and the relative increase is greater for lighter animals (Lees et al., 2013; Snyder and Carello, 2008; Tullis and Andrus, 2011). Energy expenditure while moving on a gentle downhill slope is typically lower than on the flat (e.g. Armstrong et al., 1983; Fancy and White, 1987; Taylor et al., 1972), though not for all species (Yousef et al., 1972). However, once the angle of decline becomes sufficiently large, then energy costs inevitably rise (Minetti et al., 2002); at this point the energy cost to support and control the body as it moves downhill apparently supersedes the savings made by converting potential energy to kinetic energy. Some animals will change their manner of locomotion to take full advantage of a downhill; Adelie penguins are more efficient descending a slope when they toboggan on their fronts (Wilson et al., 1991).

Environments, of course, are complex, and a number of other variables can also modulate the costs to move. Weather is an obvious example. Running into the wind increases costs for humans (Davies, 1980), though beyond this study the effects of wind on transport costs have been investigated mostly in volant birds (Elliott et al., 2014; Riotte-Lambert and Weimerskirch, 2013), which are likely to be more greatly affected by wind strength and direction than are terrestrial animals. Clearly, all these terrain and environmental factors can interact with each other. However, little empirical work, particularly on terrestrial animals, has been done to quantify how multiple parameters (e.g. incline and substrate properties) combine to determine energy expenditure (Irschick and Jayne, 1999; Shepard et al., 2013; Williams et al., 2014).

Load carrying and non-linear walking

Load carrying represents another major influence on walking costs: there is an energetic price to pay for an animal to transport an additional mass. For example, human mothers expend more energy

to walk with an unborn child in the final stages of pregnancy (van Raaij et al., 1990) and also pay a cost to carry them postpartum (Wall-Scheffler et al., 2007; Watson et al., 2008). And knights of old would have consumed considerable extra energy for the privilege of walking into battle under shining armour (Askew et al., 2012). Initially, animal data indicated that the increase in cost for an animal to move when carrying an additional weight on the body was in direct proportion to the increase in effective body mass (Taylor et al., 1980). However, Kram (1996) later found that rhinoceros beetles buck this apparent trend, being far more energetically efficient load carriers than any species measured previously. More recently, some other species have demonstrated the capacity to carry weights at an extra energy cost lower than that of supporting their own bodies, so long as the load is suitably positioned on the body (Marsh et al., 2006; Tickle et al., 2013). Indeed, different ways of carrying the load can greatly affect the transport costs (Bastien et al., 2005; Lawrence and Stibbards, 1990; Quesada et al., 2000; Watson et al., 2008). The final twist to this topic is that some animals have anatomical adaptations protecting them from incurring any costs owing to load carrying; wallabies can transport a large young in their pouch with negligible increases in energetic costs because they access greater elastic return from their hind-limb tendons when carrying their offspring (Baudinette and Biewener, 1998).

Often, animals do not move through their habitat steadily and linearly but rather vary their speed and choose tortuous routes. Recent work has demonstrated that when an animal's direction of travel is not linear, its energy costs are exacerbated (Fig. 3) (Amélineau et al., 2014; Boisclair and Tang, 1993; Krohn and Boisdair, 1994; Wilson et al., 2013b). For example, imagine a person taking a stroll along winding paths in a forest. While walking in a straight line at 1.67 m s^{-1} – a speed within the typical range for walking – they might consume approximately 1.2 l O$_2$ min^{-1}. However, along winding paths they may be making 45-deg turns on average every 10 s or so, and this would increase their energy expenditure by ~10%. Making 45-deg turns 10 times every minute would increase their energy expenditure by >15%, and if those turns averaged 90 deg, the increase in energy expenditure would be closer to 30%. Animals also tend to move intermittently, either stopping periodically or changing speed (Girard et al., 2001 and references therein; Kramer and McLaughlin, 2001). Similar to a force being required to exact a change in direction during an animal's motion (Wilson et al., 2013b), forces must act during acceleration and deceleration when the animal changes speed or halts, though there has been little empirical work undertaken to quantify this (but see Boisclair and Tang, 1993; Krohn and Boisdair, 1994; Zamparo et al., 2014). Thus, locomotion at varying speeds also demands greater energy expenditure. We can therefore expect that animals on the move do not deviate from their heading and speed without good reason, such as to increase the probability of finding food or to evade a predator (Wilson et al., 2015).

Energetics driving ecology

Studies that perturb single variables and measure their effect on NCOT$_{min}$ under controlled laboratory conditions have greatly enhanced our understanding of the energetics of animal locomotion. However, the eclectic terrains and environmental factors affecting NCOT$_{min}$ that have been investigated thus far represent only a proportion of the plethora of extrinsic influences on the costs of locomotion for any particular species. Furthermore, many of those terrains and environmental factors are likely to exhibit strong interaction effects (for example, the cost of walking uphill will be exacerbated by slippery conditions but perhaps
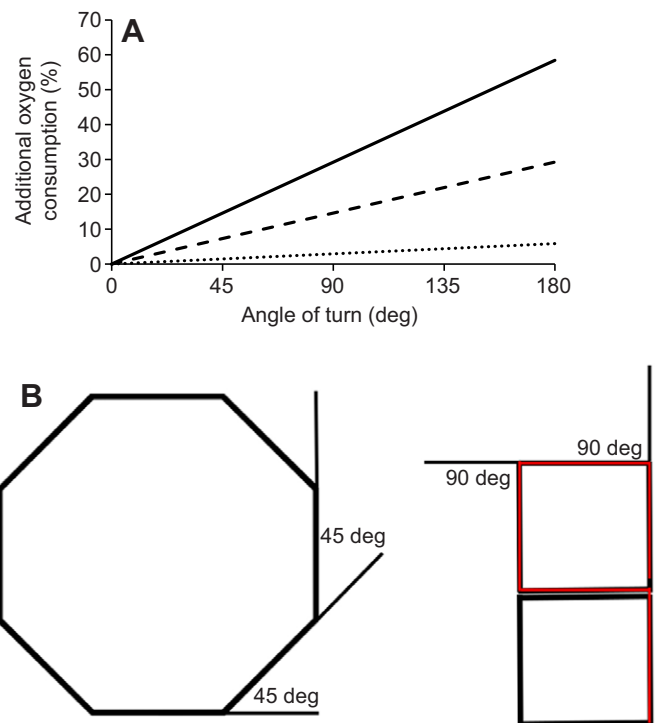
Fig. 3. The energy expenditure incurred during walking increases due to turning. (A) Additional oxygen consumption (a measure of energy expended, %) is related to the angle of the intermittent turns undertaken by people walking at 1.67 m s^{-1}. The additional oxygen consumed increases with both the angle of the turn and the frequency of turning (dotted line, 1 turn min^{-1}; dashed line, 5 turns min^{-1}; solid line, 10 turns min^{-1}). Derived from the full data set presented in Wilson et al. (2013b). (B) Some of the paths taken by participants in the study by Wilson et al. (2013b), enabling comparison of the difference in walking costs as a result of different turning angles. Note that within and between paths the walking distances between turns are equal. The red lines in the 90 deg path indicate part of the route walked by the participants around the path. Based on schematics provided by Owen Bidder (Stiftung Tierärztliche Hochschule Hannover, Institut für Terrestriche und Aquatische Wildtierforschung).

attenuated by a following wind). This raises the obvious concern that empirical measurements of NCOT$_{min}$ obtained from controlled experiments may not provide sufficient information for us to accurately estimate energy costs in the complex reality of the natural environment. As Williams et al. (2014) put it, GPS tracks do not recognise variability in topography, substrate and weather.

What alternative experimental avenues are available? We might reasonably expect to ascertain the energetic effects of the most influential extrinsic factors by measuring a free-living animal's energy expenditure as it traverses a measured environment. We could record estimates of an animal's energy expenditure in the field at a suitably high temporal resolution through a variety of methods (Green, 2011; Halsey, 2011; Halsey et al., 2011), and thus with sufficient data points and detail about the current landscape and environment, regress the former against the latter to quantify the energetic influences of the various extrinsic factors. However, such a study would be technically and logistically demanding; to the best of my knowledge, such quantification of the effects of multiple environmental factors based on empirical measures of energy expenditure (proxies) has not yet been undertaken.

Yet we may already be at the point where further quantification of the effects of environmental factors on single species, even if validated in the field, offers little beyond an incremental increase in our understanding of the resistivity of landscapes to locomotion.

Instead of further refining what we know about the effects of landscapes on $NCOT_{min}$, we should focus our investigation on how the influence of the landscape on an animal's movement costs affects its ecology, i.e. how the landscape affects the way in which the animal utilises the surrounding environment. In this vein, Wilson et al. (2011) and Shepard et al. (2013) progressed and popularised the concept of the 'energy landscape'. Animals navigate pathways through the energy landscape, which is shaped by the lie of the land along with, for example, the details of its terrain and the weather. They will tend to take routes through the energy landscape that reduce their movement costs, and this will underlie movement patterns at large and small spatio-temporal scales, such as predator–prey interactions, preferred foraging sites and migration routes (Shepard et al., 2013), and probably also invasion routes. Rees (2004) calculated that mountain paths in Wales used by hikers typically minimise metabolic costs rather than time; this is perhaps the first paper to demonstrate the influence of the energy landscape on movement patterns. Newmark and Rickart (2012) showed that ungulates choose routes through Red Butte Canyon that steer clear of steep slopes and heavily forested areas, and interpreted this as a motivation to economise energy use. Wall et al. (2006) provide a concise and striking example of generating an animal's 'energy landscape' to interpret its ecology, albeit with debatable conclusions. They reported that an elephant herd foraged everywhere in their territory except on a prominent hill, despite the presence of lush vegetation at its peak. Wall et al. (2006) argued that this was because of the excessive energy that would be lost during the ascent of the hill; given the great size of the elephants, the energy landscape of the hill was so high that traversing it would cost them too much energy to make exploiting the vegetation atop energetically worth their while. Although other explanations for these movement patterns can be argued, Wall et al. (2006) present one of the few case studies to date showcasing how the landscape's effects on movement energy costs could have stark consequences for the way an animal traverses its habitats.

Choices made by the optimising animal: the individual energy landscape

Despite the importance of energy to an animal, its judicious expenditure may not always be the priority. Short-term optimality typically involves trading off various currencies that include, alongside energy costs, time costs and predation risk (Kacelnik et al., 1981; Mangel and Clark, 1986; Tolon et al., 2009). Thus, certain scenarios may preclude an animal from prioritising energy economy; out-running a predator, for example, is clearly essential for maximising fitness and is less likely to be accomplished at speeds that minimise transport costs. Given that animals will, at least sometimes, trade-off energy economy against other important considerations by moving at energetically sub-optimal speeds, I suggest that the energy landscape concept can be taken a step further by incorporating the trade-offs made by the optimising animal. Although the energy landscape describes how the terrain and other external factors influence the energy costs of movement for an animal, this does not account for variations in speed employed by that animal, which also affects its movement costs. Thus the true energy landscape for a given animal must reflect its chosen locomotion speeds across that landscape.

This can be described as the animal's 'individual energy landscape'. Within energetic limits, an animal's individual energy landscape is self-modified, in that it changes depending upon the locomotion strategy adopted by the animal at the time (Fig. 4). The topography of the individual energy landscape is at its lowest when
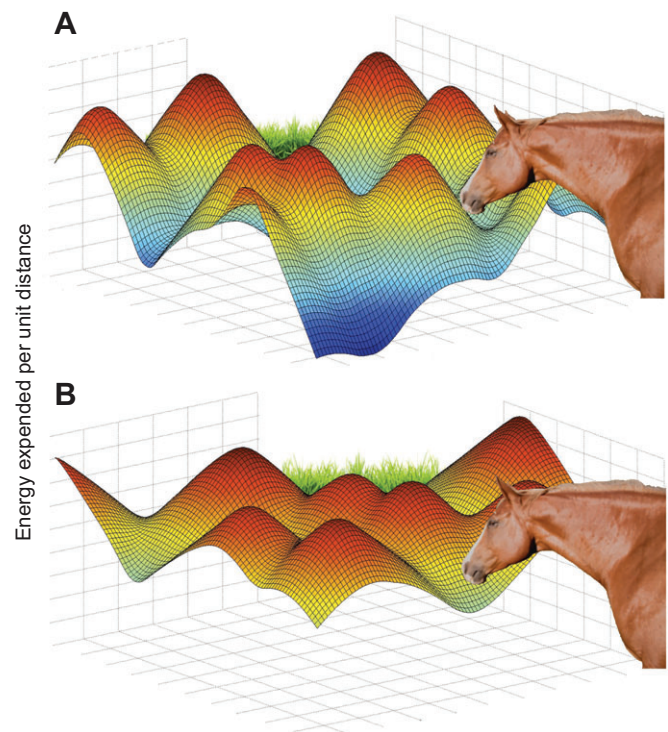
Fig. 4. The concept of the individual energy landscape. This landscape represents variation in space in the energy cost to move a unit distance; reds indicate high costs and blues represent low costs. The minimum energy costs that can be incurred by an animal to move across a geographical landscape by a given route are defined by physical factors such as the substrate and slope of the terrain. However, the energy costs actually incurred by that animal can differ depending upon the decisions it makes predominantly about the speeds at which to traverse the landscape. An animal may wish to minimise its costs to move in order to maximise energy available for reproduction or to minimise the effects of fatigue. For example, if a horse intends to move to a food patch but is not under a time constraint, it may opt to walk at an average walking speed, which is likely to be energetically economical for the given terrain (Hoyt and Taylor, 1981) (A). It may also choose an indirect route across its individual landscape that is nonetheless energetically more economic than the most direct route such that the energy spent to reach the food patch is further reduced. (B) In contrast, if, for example, the horse opts to trot at a high speed (less economical for horses, which display a curvilinear $NCOT_{min}$ within gaits; Hoyt and Taylor, 1981; see also Fig. 1B) in order to reach the food patch quickly, then all routes to cross the landscape, at least on average, become more energetically expensive. The energy expended to get to the food might be further increased if a direct route is taken to further reduce the time taken (for example, if the direct route included inclined terrain). Because of possible interactions between, for example, movement speed, slope angle and the substrate underfoot, we would typically expect the landscape to vary in response to movement speed in a more nuanced fashion than simply raising or lowering a consistent amount across the surface. For instance, in the present example, although the majority of the landscape is raised in B, indicating higher energy costs to cross the landscape at a high trotting speed, there are nonetheless a number of peaks in A where that point on the landscape cannot be traversed more economically by moving at slower speeds. This could be the case, for instance, when moving into high winds or travelling downhill.

the animal has elected to vary its speed of travel such that at any given point on the landscape surface it is minimising its costs to move, i.e. it is moving across the landscape at the lowest energy cost possible. However, in the wild at least, where various interests can compete, sometimes an animal may select a movement speed that does not optimise energy economy, sacrificing this currency for an alternative (Reilly et al., 2007). For example, if time is of the essence, perhaps because the animal is pursuing prey or attempting

to reach a food patch before it is depleted by conspecifics, speeds higher than that associated with optimum energy expenditure may be necessary (Wilson et al., 2002). Under certain foraging circumstances, when energy uptake is the focus, speeds below the optimum may be suitable, for example, to increase the proficiency of spotting prey or snapping it up (Hirsch, 2010; Wilson et al., 2002). When predator avoidance is to be prioritised, slower speeds or intermittent locomotion may also decrease an animal's chance of being detected. In all of these cases where the animal is not optimising the economy of its energy expenditure, instead trading off energy economy for gains in another currency, its individual energy landscape becomes raised (Fig. 4B); the animal accepts using extra energy as the cost of prioritising another factor over locomotion economy while it is on the move.

Considering animal movements and the associated energy costs through the concept of the individual energy landscape, animals might be expected to be more judicious with energy expenditure when energy availability is low. In turn, they might be predicted to move through relatively low individual energy landscapes. This would be associated with a host of behaviours that optimise the energy economy of movement. Such behaviours include the geographical paths taken, which may incorporate the use of transportation networks (Perna and Latty, 2014), the speeds of movement, and perhaps also whether movement is undertaken in a group. In contrast, less emphasis on energy economy might be exhibited where energy availability is high or perhaps when an animal is emaciated but is aware of the likely short-lived presence of a nearby food source. Under such circumstances, animals may exhibit a disregard for movement behaviours that are energetically economic, represented by an elevated individual energy landscape.

The flexibility in the movement strategy available to an animal to exact such trade-offs between energy expenditure and other important factors such as predation, resource acquisition and sociality will depend on the lie of the energy landscape and the animal's physical capacity to traverse it (e.g. Abrahms et al., 2015). In terms of the landscape, for instance, it may be difficult to justify deviations from the energetically optimum route if the energy loss will be great, for instance if the energy landscape is composed of clear valleys between mountains, such as may be created by animal transport networks (Newmark and Rickart, 2012; Perna and Latty, 2014) exemplified by packed paths through deep snow (Crête and Larivière, 2003). Thus, the movement behaviours of animals through certain landscapes may be highly predictable regardless of an animal's present objectives if certain routes and speeds are considerably more economic than alternatives. In terms of physical capabilities, an animal has greater scope to trade off energy economy if it has the athletic capacity to traverse the energy peaks of the landscape. Thus ageing animals or individuals otherwise relatively limited in their physical capacity may exhibit a constrained individual energy landscape, always moving at the same speeds, taking the same routes and in other ways generally presenting repetitive movement behavioural patterns regardless of context.

Experiments involving motivations to move around a landscape (most obviously for food) could assess changes in movement behaviour through that landscape depending upon factors such as the animal's body condition, competing concerns such as predator avoidance, and levels of conspecific competition. The effects of landscape structure, the presence of transport networks or animal physical condition on constraining the plasticity of movement could also be investigated. Such experiments could also potentially quantify the resultant changes to energy cost, probably through the use of animal-borne data loggers (Cooke et al., 2004). Such data

could supersede isolated measures of energy expenditure of animals exposed to a consistent and simplistic locomotion scenario such as are inherent in treadmill-based protocols or even treadmill-equivalent studies in the field. Furthermore, if energy intake could also be measured, then net energy gain – a key measure of animal fitness – could be calculated. In turn, the ultimate effect of the behavioural decisions made by an animal that change its individual energy landscape might be quantified by net energy gain.

Conclusions

The choices animals make, albeit subconsciously, to optimise their behaviour result in trade-offs between key variables such as time, energy and predator avoidance. When an animal is moving within its environment, the lie of the land and nature of the terrain are key in influencing the route it takes and the speed at which it travels as it seeks to balance these trade-offs. This influence of terrain is largely due to the varying energy costs of locomotion associated with the environment, which define the animal's energy landscape. However, for any chosen route, an animal can optimise the energy cost of traversing the terrain – it can limit the height of its individual energy landscape – by moving across the landscape at the most energy-efficient speeds. Conversely, it will accept a more 'mountainous' individual energy landscape if it is optimising a variable other than energy expenditure. Thus, understanding how an animal's movement costs are governed by its morphology and physiology, coupled with the terrains and environments it inhabits, and then how those costs are modulated by its movement patterns, is key to understanding the 'energy envelope' within which the optimising animal must make its choices. In turn, this energy envelope provides the fundamental framework within which the animal's behaviour can be assessed. Further studies measuring the metabolic rate of terrestrial animals during locomotion under perturbed conditions (e.g. variations in substrate type and angle, and weather conditions) will refine our ability to quantify their movement costs. There are also potential as yet unexplored key influences on locomotion energy costs, such as group movement and group position, and intermittent movement. Investigating the interactions between multiple key factors will be fundamental to better model the real world. However, to understand how locomotion energy costs influence an animal's ecology as it strives to optimise its fitness, we must turn our attention to how it adjusts its movement behaviours and, in turn, how these combine with the energy landscape to affect an ultimate outcome: net energy gain. Only then, for example, can we start to understand how species of similar sizes can experience vastly different energy outlays during locomotion without apparent variation in their evolutionary fitness.

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