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Synthesis

Energy Landscapes Shape Animal Movement Ecology

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abstract: The metabolic costs of animal movement have been studied extensively under laboratory conditions, although frequently these are a poor approximation of the costs of operating in the natural, heterogeneous environment. Construction of "energy landscapes," which relate animal locality to the cost of transport, can clarify whether, to what extent, and how movement properties are attributable to environmental heterogeneity. Although behavioral responses to aspects of the energy landscape are well documented in some fields (notably, the selection of tailwinds by aerial migrants) and scales (typically large), the principles of the energy landscape extend across habitat types and spatial scales. We provide a brief synthesis of the mechanisms by which environmentally driven changes in the cost of transport can modulate the behavioral ecology of animal movement in different media, develop example cost functions for movement in heterogeneous environments, present methods for visualizing these energy landscapes, and derive specific predictions of expected outcomes from individual- to population- and species-level processes. Animals modulate a suite of movement parameters (e.g., route, speed, timing of movement, and tortuosity) in relation to the energy landscape, with the nature of their response being related to the energy savings available. Overall, variation in movement costs influences the quality of habitat patches and causes nonrandom movement of individuals between them. This can provide spatial and/or temporal structure to a range of population- and species-level processes, ultimately including gene flow. Advances in animal-attached technology and geographic information systems are opening up new avenues for measuring and mapping energy landscapes that are likely to provide new insight into their influence in animal ecology.

Keywords: cost of transport, migration, track tortuosity, accelerometry, biotelemetry, isoenergy polygon.

Introduction

Natural selection will tend to favor animals that move efficiently, which leads to widespread energy-saving mechanisms, be they biomechanical, physiological, or behavioral (e.g., the selection of travel speed, gait, or route; Tucker 1970; Dickinson et al. 2000; Nathan et al. 2008). The question of what represents an efficient movement strategy must, however, be examined in relation to the environment that is being traversed, because the overall cost of a given travel speed or gait, for example, may vary according to the route or time of travel (Furness and Bryant 1996; Wall et al. 2006; Sapir et al. 2010). This environmentally dependent variation in the cost of transport, driven by variation in parameters such as incline, substrate type, vegetation, current speed, or direction, is termed the "energy landscape," following Wilson et al. (2012). The energy landscape may vary in space and/or time, providing compelling energetic reasons for animals to adapt their movement strategy accordingly.

To date, the energy savings available by modulating movement in relation to the environment have been difficult to define because of the discrepancy between the constrained laboratory conditions under which the metabolic costs of locomotion are measured (Dickinson et al. 2000) and those encountered in the wild. Yet animals across the size spectrum, including those with the weakest movement capacity (Reynolds and Reynolds 2009; Chapman et al. 2010), are known to alter their behavior in relation to the environment to both exploit opportunities for energy gain and minimize movement costs. Indeed, the energy savings available are likely to provide strong selective pressure for animals to respond to the energy landscape, whether they are undertaking long but infrequent migrations or shorter daily movements in which small but regular savings may still result in substantial cumulative energy gains (Alerstam 1993; Shepard et al. 2011). Although responses over large scales are well documented, with millions of animals adjusting the timing and routes of spectacular migrations to benefit from particular air or water currents (Jones et al. 1979; Liechti et al. 2000; Bohrer et al. 2011), small-scale tactics have been

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documented in only a few instances (e.g., Wall et al. 2006; Sapir et al. 2011), primarily when the decreased costs of locomotion are visually obvious (Mandel and Bildstein 2007). Such widespread, nonrandom use of the environment across spatial scales is likely to have a profound effect on a range of population processes, from the formation of migratory flyways (Mandel et al. 2008) to species distributions (Davies et al. 2009), metapopulation dynamics, and the spread of disease (Si et al. 2009). Quantification and visualization of energy landscapes could therefore provide insight into physical factors that affect these processes.

This study documents how the physical properties of the environment affect the costs of transport in animals and advocates the construction of geographic information system (GIS)–type energy landscapes, which provide a framework with which variation in animal movements can be understood or predicted over varying spatial and temporal scales. The critical importance of energy landscapes in animal ecology is addressed through a select review of examples in which the costs of movement have been measured in relation to defined environmental parameters. Concepts for quantifying and visualizing the energy landscape are introduced, along with tools for examining least-cost movement pathways. The latter provides a quantitative basis for the links between the physical characteristics of the environment, capacity for movement, and observed movement paths, which form a key part of a recently proposed conceptual framework for the mechanistic understanding of organismal movement (Nathan et al. 2008). The construction of energy landscapes also provides insight into the importance of other key drivers of animal movement, such as predation, food abundance, physiological state, and access to information (e.g., on spatial variation in movement costs or risk), particularly where animal movements deviate substantially from low-cost strategies.

Toward a Definition of Cost-Effective Animal Movement

The energetics of animal movement using power or mass-specific power (values given in W or W/kg, respectively) are often couched in terms of cost of transport (COT) where the energetic cost is calculated per unit distance traveled (J/m or J/kg/m; Schmidt-Nielsen 1984). The minimum cost of transport (COT_{min}) is important in animal movement ecology, because it represents the conditions under which an animal uses the minimum energy to cover a defined distance (normally defined by the speed; Tucker 1970). COT changes with speed, moving toward an infinite value as the speed decreases toward zero because, although power costs for actual locomotion decrease with speed (with the exception of flapping flight; see Pennycuick 2008), the relative proportion of the resting metabolic rate generally increases with decreasing speed (distance traveled per unit time; fig. 1*A*). Commonly, movement in terrestrial, aquatic and aerial environments is examined for rectilinear, level movement (Dickinson et al. 2000) on or in a laboratory medium that controls for parameters such as incline and substrate type but which bears little resemblance to almost anything the animals might encounter in the wild. Here, we adopt the laboratory scenario as our standard, but detail, where appropriate, any variance as multiples of it.

Variable Costs of Transport with Landscape

The physical form of the environment will result in movement costs that may produce higher or lower energy requirements than the laboratory norm. Terrestrial animals negotiate a relatively static energy landscape in which the environment changes little or not at all over time (but see table 1). Nonetheless, spatial heterogeneity can be substantial, and ascribed values for COT will accord with the precise track taken by animals to move through it. Air and water are dynamic fluid energy landscapes, in which flow may change substantially from one moment to the next and affect COT even if animals repeatedly choose one particular route.

Static Energy Landscapes

Within static energy landscapes, we propose three major divisions of factors that influence COT, which may occur in any combination or in isolation. Although there is little information on the COT according to variation in static energy environments for animals in general, there has been work on how the landscape properties affect COT in humans and other vertebrate examples, and we use this for illustration of general phenomena.

Substrate penetrability (in which the substrate is defined as the medium over or on which an animal moves) determines the extent to which an animal will sink into the ground and deform it. This affects the metabolic costs of movement, because work is done in deforming the substrate, and the efficiency of the positive work performed by the muscles and tendons is reduced (Lejeune et al. 1998). Values of penetrability will vary in relation to the loading of the body surface in contact with the substrate (typically, this will be foot loading). Some substrates, such as sand, that display both solid and fluid-like behavior (Maladen et al. 2009) are expected to be costly for a range of species. Humans walking on soft sand have an energy expenditure that is 2.1–2.7 times that of humans walking on solid rock (White and Yousef 1978; Lejeune et al. 1998), with a COT that changes accordingly. Equivalent conditions for arboreal species occur as a result of branches bending, with the energetic costs of movement typically increasing with compliance (Alexander 1991), and locomotor performance in snakes, lizards, and mammals is also reduced (although see Bonser 1999; Byrnes and Jayne 2010 for the importance of risk in branch selection; and Thorpe et al. 2007 documents a case in which energy can be recovered from compliant branches).

In some scenarios, it is difficult to separate the costs of deforming a substrate from those of moving through a superstrate (see below for a definition of superstrate). For instance, the power costs of locomotion in snow for caribou *Rangifer tarandus* increase exponentially with snow depth (Fancy and White 1987), yet this is attributable to the combined effects of substrate penetrability and the drag imposed on the limbs by the superstrate.

The superstrate may be defined as any material against which an animal must push to move. For a ground-moving vertebrate, this will be material that projects above the substrate, such as tall grass. This alters the COT, because extra energy is required to displace or deform the material, and costs will generally increase with factors such as superstrate height, density, and rigidity. For instance, humans walking through light and heavy brush have power requirements that are 1.2 and 1.6 times higher than those of humans walking on open ground (Knapik et al. 2004). Locomotion within sand, soil, and sediments by vertebrates and invertebrates can also be considered in this framework, although the costs of burrowing in these viscoelastic media are less well understood (Maladen et al. 2009; Dorgan et al. 2011).

The superstrate can also modulate the COT by influencing traveling speed (fig. 1*A*). Small animals may be particularly sensitive to factors that impede or slow locomotion because of the relatively large contribution of their resting metabolic rate to their overall COT (Taylor et al. 1972), which results in a sharp increase in COT as speeds decrease toward zero (Full and Tullis 1990). In fact, this may have acted as a driver for the evolution of trichomes (hairs) on plants as an insect deterrent, because,

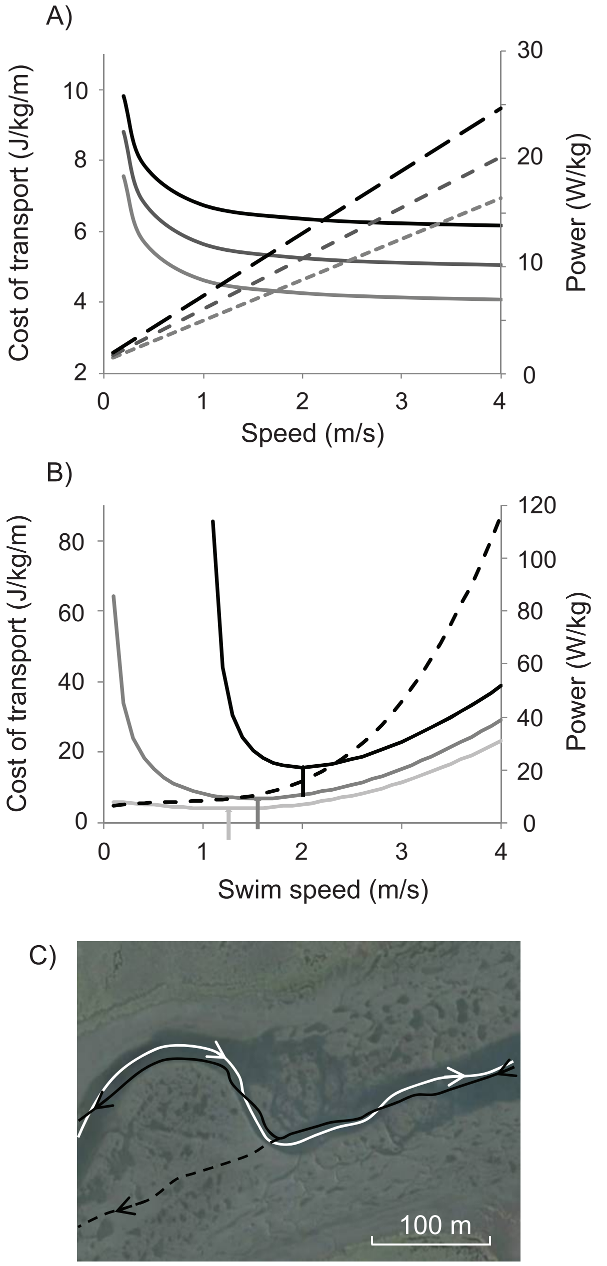

Figure 1: *A*, Power requirements for humans running (dashed lines) increase with incline. Requirements are given for movement on a flat surface (light gray) and on 5% and 10% slopes (dark gray and black lines, respectively; Margaria et al. 1963). The cost of transport (COT) for each scenario is given by solid lines. *B*, Power requirements for swimming Humboldt penguins (dashed black line) increase according to a power function of swim speed (Luna-Jorquera and Culik 2000), giving the costs of transport a characteristic U shape (solid dark gray line). This can be used to calculate the COT with and against a 1 m/s current (light gray line [COT_{min} = 4 J/kg/m, as indicated by the light gray arrow] and black line [COT_{min} = 15.8 J/kg/m, as indicated by the black arrow], respectively), demonstrating the advantage in changing swim speed according to current direction and strength. *C*, Congeneric Magellanic penguins nesting in San Julian Bay, Argentina, commuting between their breeding sites and the sea also alter route and travel mode according to tidal current strength. During the ebb tide, birds leaving their colonies (white trace) dive little, being washed down in the middle of the rivers where the flow is fastest. Birds returning from foraging at this time (solid black trace) swim along the inner side of river sweeps where flow rates are lowest. Even so, when traveling against a current of 1 m/s, these birds have a COT approximately double those of birds moving with the current. When contra-current conditions become too extreme, birds walk (dashed black trace). The situation is reversed with incoming tides (after Wilson et al. 2001).

Table 1: Examples of drivers and temporal scales of variability in energy landscapes

Driver, example	Time scale	Example of changing landscape
Biological:		
Animal movement	**Seconds–hours**	**Vortex wake generation**
Trail use	Days–years	Reduced superstrate
Vegetative growth	Days–months	Increased superstrate
Meteorological:		
Wind variability	**Seconds–minutes**	**Small-scale gustiness**
Insolation	**Minutes–hours**	**Thermal generation**
Precipitation	**Minutes–hours**	**Increased flow in streams**
Precipitation	**Minutes–hours**	**Altered substrate penetrability**
Gravitational:		
Tides	**Hours**	**Variable current vectors**
Tides	**Hours**	**Intertidal habitat availability**
Geophysical:		
Sedimentation	**Hours–millennia**	**Water vectors, slope angles**
Erosion	Days–years	Slope angle, wind vectors
Mountain formation	Millennia	Slope angle, wind vectors
Anthropogenic:		
Vehicle movement	**Seconds–hours**	**Bow-wave generation**
Roads and trails	Years–centuries	Reduced substrate penetrability
Buildings	Years–centuries	Barrier formation, flow vectors

Note: Boldface type indicates examples of changes in more dynamic energy landscapes (i.e., those in or affected by fluid media, where the variability extends to shorter temporal scales).

although trichomes may impale insects (Levin 1973), such hairs also increase the COT substantially by simply slowing the insect's rate of progress along the plant surfaces.

Substrate topography ranges from flat surfaces, through uneven terrain, to steep inclines. Uneven surfaces (where the topography varies within a body length of the animal) entail additional work relative to flat surfaces, because limbs must be lifted higher, and because energy is expended in increased muscular contraction for enhanced limb stability. With true inclines (where the slope of the terrain continues for several body lengths), work is done because animals have to increase their potential energy as they move up a slope (although even movement down a slope may result in a higher COT than movement on a flat surface; Minetti et al. 2002). Humans walking up (solid substrate) slopes experience an increase in COT with slope angle (fig. 1*A*), so that a 45° slope has a COT that is more than 17 times that of level ground (Minetti et al. 2002).

Animals climbing slopes must raise their body mass, and although the mechanical work required to lift a given mass a specific vertical distance does not vary with animal size, the relative increase above resting metabolic requirements for the task varies allometrically, being greater for larger animals (Taylor et al. 1972). This explains why there is no detectable difference between the rate of oxygen consumption for a mouse *Mus musculus* running on level ground compared with one running on an incline of 15°, whereas for chimpanzees *Pan troglodytes*, the slope of oxygen consumption against speed doubles (Taylor et al. 1972). Because the relative costs of moving up inclines vary with body size, even small inclines may represent barriers to the movement of larger organisms (Wall et al. 2006). Indeed, an analysis of movement paths across 130 animals, ranging from a 0.025-kg mouse to a 680-kg buffalo, showed that trail angle decreased as a function of slope angle and the mass of the animal in question (Reichman and Aitchison 1981). Ultimately, capacities or energetic costs of moving up a slope may prohibit passage, so that animals must choose routes around the slope (Wall et al. 2006), with the final COT dependent on the extent of the deviation and its terrain (fig. 2).

Dynamic Energy Landscapes

Fluid media are, in general, highly dynamic, with movements driven by physical and chemical gradients, gravity, and Coriolis forces as well as interaction with other fluids (e.g., wind on water) and other moving bodies. Predictable elements occur within these energy landscapes because of the regularity of tidal, diel, and seasonal cycles, with short-term variance, from seconds to hours, superimposed upon them (e.g., driven by heating effects). The dynamic nature of these energy landscapes is likely to cause greater temporal and spatial variability in associated behavioral modifications, which serve to both extract energy from the environment (Chapman et al. 2010) and minimize work

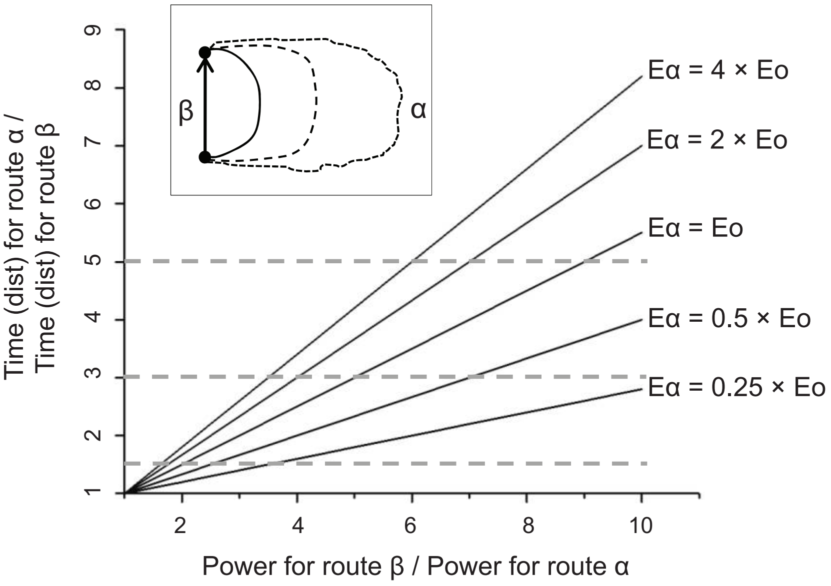

Figure 2: Role of energy landscapes in structuring route selection. As the cost of straight-line travel between two points increases (route β in the inset), so animals are expected to deviate from this path (route α in the inset), until the costs are energetically equivalent. The benefit of deviating from the straight line increases with the margin between transport costs (E_α) and resting metabolic costs (E_0), as represented by the series of lines (see app. A). Inset shows deviations corresponding to 1.5, 3, and 5 times the straight-line distance (gray dashed lines), illustrating the extent to which small changes in the modeled parameters can modify the route taken.

done against it. We suggest three main ways in which these environments may impact the costs of movement, which may vary in combination or in isolation.

The fluid flow vector has both a horizontal and a vertical component, both of which profoundly affect movement costs. For swimming animals, the minimum COT is particularly sensitive to horizontal current speed, because power costs scale exponentially with travel speed (Luna-Jorquera and Culik 2000; fig. 1*A*). For flying animals, the curve of power costs against forward speed is U shaped (Pennycuick 1969), with costs increasing exponentially above the minimum power speed. The $\mathrm{COT}_{\mathrm{min}}$ (equivalent to the maximum range speed for flying animals, V_{mr}) will also increase with the speed of any current moving against a flying animal, so the simplest strategy for animals moving in fluids (excluding those that hover) is to travel when the fluid direction is in line with their preferred direction of travel and remain stationary when it is not (Chapman et al. 2011). This strategy is widespread (Jones et al. 1979; Albert 2007; see Gill et al. 2009 for an analogous scenario in aerial movement), and even invertebrate larvae may use selective tidal stream transport to facilitate dispersal (Forward et al. 2003). Animals also adapt their horizontal movement path in relation to current speed, rather than just presence or absence of current or current direction. For example, Humboldt penguins *Spheniscus humboldti* have a $\mathrm{COT}_{\mathrm{min}}$ that increases by a factor of four when they swim against a 1 m/s water current, compared with swimming with the current (fig. 1*B*). It is presumably these variable costs that modulate the foraging paths taken by congeneric Magellanic penguins *Spheniscus magellanicus*, which preferentially swim where the tidal currents are weakened by their interaction with the substrate when swimming against the current but choose routes away from the substrate when moving with the current (fig. 1*C*; Wilson et al. 2001; McElroy et al. 2012). This demonstrates how animals capitalize on changes in fluid speed associated with boundaries to save energy.

Animal movement strategies in relation to the vertical component of the flow are most obvious in flying animals; for example, many soaring birds use wind that is deflected upward by a slope to offset (or exceed) their sink rate and thus maintain altitude (or rise) without flapping (fig. 3). In contrast, birds on the leeward side of a hill are subject to negative vertical vectors because downdrafts require an increase in power to stay aloft (fig. 3). A red kite *Milvus milvus*, for example, able to glide in air rising at 1 m/s on the windward side of the hill, would be forced to switch to flapping flight to maintain altitude in air sinking at the same speed on the leeward side, which is a process associated with a 3.6-fold increase in COT (estimated using Flight 1.24 freeware; http://books.elsevier.com/companions/9780123742995; see also Pennycuick 2008 for details of flight costs in downdrafts). Such consider-

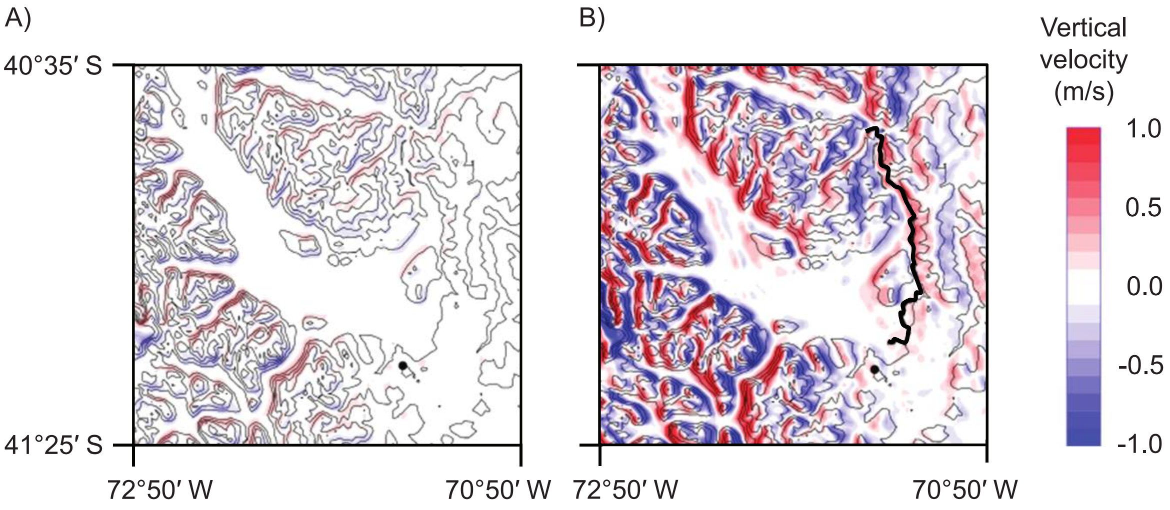

Figure 3: Energy landscape for soaring birds. Mean daytime vertical velocity of air over a section of the Andes for December 31, 2011, at (*A*) 1200 and (*B*) 1500 hours local time, as predicted by a numerical reanalysis model for flow over complex terrain (3DVOM; Vosper 2003). At Bariloche airport (black dot), the wind was from the northwest for both scenarios, varying only in mean hourly speed over the 3-h period from (*A*) 18.5 to (*B*) 37 km/h. Color shading indicates the vertical velocity (units m/s) at ~100 m above ground level. Black line in *B* indicates the flight path of a condor at 1845 hours as recorded by GPS (E. L. C. Shepard and S. A. Lambertucci, unpublished data). This bird clearly favored the windward slopes (red areas) and avoided flying in the lee (blue areas).

ations should be relevant for all flying animals, whether they are conventionally described as soarers or not (Sapir et al. 2010), although the energetic advantages are greater for larger animals, because the power requirements for flapping flight increase disproportionately with body mass (Pennycuick 2008).

Importantly, although it is difficult to quantify, slope lift is produced by much smaller obstacles than hillsides, including jetties, houses, trees, and hedges (which will generate different energy landscapes according to the amount of foliage), and animal movement patterns are likely to be affected accordingly (Williams et al. 1992). Indeed, the occupation of coastal towns by gulls may be partially explained by onshore winds hitting buildings rather than food abundance and nest-site availability alone. Other sources of vertical air currents include thermals, which are actively exploited by animals as diverse as aphids and eagles (Reynolds and Reynolds 2009; Duerr et al. 2012). Indeed, thermals generated by man-made features are also likely to affect space use by a variety of animals (Mandel and Bildstein 2007).

From microscale eddies to ocean basin circulation, all flows are turbulent at sufficiently large scales, with laminar cells embedded within them. Thus, the irregularity of the flow experienced by an animal (i.e., fluid vector variability) depends on the animal's size in relation to these cells. Animals can exploit eddies with dimensions roughly equivalent to those of their own bodies; for example, a range of salmonids engage in flow-refuging behind stones (Heggenes 2002), and fish exploit vortex wakes produced by conspecifics (Liao et al. 2003). However, turbulence can also increase the COT. For instance, individuals from a range of bee species extend their hind legs during flight in turbulent conditions, which improves roll stability but increases power requirements by 30% (Combes and Dudley 2009).

The pressure of a fluid as a result of an animal's vertical position within the environment can also affect the COT. In aquatic environments, hydrostatic pressure due to water depth is a key determinant of buoyancy for many animals and is also a determinant of the power they must produce to counter this (Wilson et al. 1992). Indeed, imperial cormorants *Phalacrocorax atriceps* appear to select areas with dive depths where their overall COT is minimized (Wilson et al. 2012). In the aerial environment, animals flying at higher altitudes experience thinner air and greater metabolic costs during flapping flight through reduced lift generation (Pennycuick 2008). Yet understanding the selection of flight altitude remains a complex task because of the number of environmental parameters that tend to vary with altitude, including the flow vector and variability (see above; Liechti et al. 2000), temperature (Reynolds et al. 2009), and humidity (Schmaljohann et al. 2007). Furthermore, the relative importance of the environmental variables may vary in space and time, such that migrants select different altitudes and environmental variables at different stages of their migration (Schmaljohann et al. 2007).

Practical Construction of Energy Landscapes

Practical Estimates of Costs of Movement in Wild Animals

Energy landscapes have, to our knowledge, been modeled in four studies to date. These maps of the metabolic costs of movement have explained substantial variation in the patterns of space use in African savannah elephants *Loxodonta africana* (Wall et al. 2006) and imperial cormorants (Wilson et al. 2012), as well as path selection in pallid sturgeon *Scaphirhynchus albus* (McElroy et al. 2012) and humans (Rees 2004). Movement costs in these studies have been derived primarily as a response to a single environmental parameter that is likely to represent the most important source of variation in movement costs in each case (incline for elephants and humans, dive depth in cormorants, and drag in sturgeon). Allometric equations of energy expenditure can, in many cases, inform a priori expectations of how movement costs may vary in relation to particular types of environmental features (Wall et al. 2006). In some instances, the environmental parameters most relevant to given life histories have already been investigated in terms of their effect on the cost of transport (Fancy and White 1987). Spatial variability in these costs can then be examined by mapping costs in relation to environmental variation of the parameter in question (see "Construction of Cost-Space Maps"). Use of a single resource layer may well prove useful in forming and testing hypotheses of the relative importance of different parameters. Additional data layers can then be added that estimate the cost of movement according to additional environmental variables. This type of model approach is developed for a terrestrial animal moving in a topographically variable landscape in appendix B.

The effects of environmental parameters on the costs of movement and locomotor performance are complex and interactive (Irschick and Garland 2001). Irschick and Jayne (1999) suggest that substantial gains could be made here through more realistic laboratory experiments, particularly by determining energy expenditure as a function of multiple parameters to quantify, for example, how substrate and incline interact. Nonetheless, proper generation of the energy landscape is likely to require high-resolution measurements of or proxies for activity-specific metabolic rate of wild animals.

The measurement of heart rate (Butler et al. 2004) or dynamic body acceleration (Gleiss et al. 2011) can provide powerful proxies for exercise-related metabolic rate and can be determined by loggers on free-living animals. Such estimates of power can be combined with known animal positions (e.g., from GPS data) to derive landscape-specific movement costs (Wilson et al. 2012; fig. 3). The GIS data can be used to relate these costs to environmental parameters in terrestrial habitats. For animals moving in fluids, atmospheric reanalysis models (Bohrer et al. 2011) and particle tracking models (Chapman et al. 2010) can be used to predict flow vectors. Although these approaches may not always be designed for the determination of fine-scale patterns, many of which are particularly germane to animals (Shepard et al. 2011), relatively coarse-scale environmental data can be ground-truthed using sensors on the study animals. For example, data from animal-attached accelerometers can provide insight into substrate characteristics and slope angle (e.g., in quadrupedal animals in which the body angle accords with the angle of the slope). In this way, aspects of landscape ecology and biotelemetry could be combined in an iterative approach to estimate the metabolic costs of movement in varied environments.

Construction of Cost-Space Maps

In the same way that contour plots help one to understand topography, we should aspire to produce map-based visualizations that describe the space-dependent costs of animal movement. For this, we suggest the concept of iso-energy polygons (IEPs). In a first step, we consider any animal's position defined by (x, y, z) coordinates (e.g., latitude, longitude, and altitude) and, via GIS information or otherwise, define the nature of the landscape surrounding the animal in terms of substrate characteristics for terrestrial environments or vertical vectors for fluid environments (excepting incline or horizontal fluid flow, which are included as a second step; see below). We then estimate the distance from that initial position that the animal can move using a defined amount of energy (e.g., a standardized measure, such as that amount of energy used during 1 min of resting metabolic rate [RMR] for that species). Speed can be selected using previous information on likely rates of movement or the predicted minimum cost of transport speed (Hoyt and Taylor 1981; Pennycuick 2008; Watson et al. 2011). Constant environmental conditions around the animal will result in a circle where the radius, and therefore the surface area, is defined by the cost of transport (fig. 4). Gridding such circles on conventional maps will give an initial impression of the ease and consequently optimized path of movement in relation to geographical area.

The cost of transport often changes according to direction, however, being modulated by horizontal flow vectors in fluid media and inclines in terrestrial environments. To incorporate this, we suggest that the final distance of a point from the start position in any specified direction will be modified by the ground speed of the animal (and hence

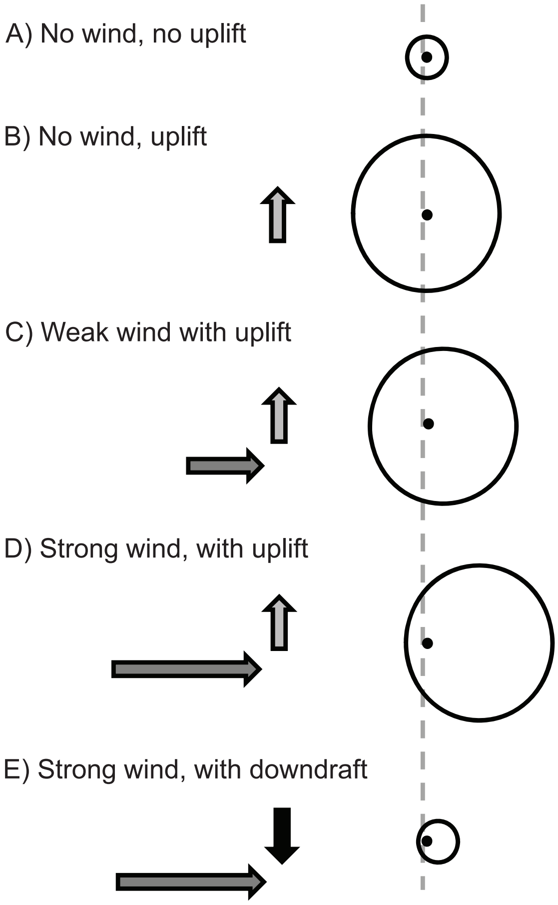

Figure 4: Schematic isoenergy polygons illustrating the form taken according to the conditions describing the energy landscape. Example is illustrated for a flying bird, where the central black point shows the considered start position of the bird (these have been aligned along the gray dashed line). Contour lines delineate the distance between the origin and the farthest point that can be reached by the bird in a given direction with a defined amount of energy, according to horizontal (dark gray arrows) and vertical (black or light gray arrows) airflow vectors. Similar isoenergy polygons can be constructed for aquatic animals or for terrestrial animals moving on slopes.

the horizontal component of the flow vector in fluid media) as well as the time taken for the animal to expend the defined amount of energy moving across (or through) the landscape. This process can elongate IEPs, depending on the directionality of the energy landscape (fig. 4).

As an example, the spatial variation in the costs of movement for a soaring bird, the black vulture *Coragyps atratus*, was visualized for a region in Patagonia with variable air flow vectors. The vertical components of the air flow vector (experienced by the bird as uplift or sink) and the horizontal components were predicted by a numerical reanalysis model for flow over complex terrain (Vosper 2003), which computes the flow for a given undisturbed wind and temperature profile. These profiles were obtained from UK Met Office forecasts for the region. The mean vertical and horizontal velocities for each grid point were computed from model outputs for the daylight hours of December 2011 and January 2012 (the provisioning period for many soaring birds in the region) with a 3-h temporal resolution. Wind directions are fairly conserved in this region, with westerly winds representing between 65% and 75% of daily observations (Paruelo et al. 1998).

IEPs were constructed by (1) deriving the cost of maintaining altitude and (2) incorporating directionality in movement costs related to the horizontal flow. With respect to the vertical component, birds must use flapping flight to maintain altitude in sinking air, and the mechanical power requirements can be estimated as the body weight multiplied by the vertical component of the speed (i.e., the sink rate) plus the power required for level flight. For the sake of simplicity, we used the speed that provides the maximum distance flown per Joule expended (the maximum range speed, V_{mr}). Both the speed and the power required for level flight were estimated using the Flight 1.24 freeware (Pennycuick 2008). The putative radius of the IEP is calculated as the energy budget divided by the power required to maintain level flight and multiplied by the maximum range speed.

When birds encounter updrafts that exceed their sink rates, they can maintain altitude by soaring. Soaring birds are able to achieve faster overall flight speeds in stronger updrafts (Pennycuick 2008; Bohrer et al. 2011), providing a mechanistic link between updraft strength and the cost of transport. Here, for simplicity, we assume that the black vulture increases its forward speed with the strength of updrafts encountered, according to the form of the glide polar, which is the function relating forward speed to sinking speed. In this case, the putative radius of the IEP is given by the total energy budget divided by the soaring metabolic rate (estimated using Flight 1.24) and multiplied by the airspeed. In both cases, therefore, the radius of the IEP is given by

$$r = V\left(\frac{E}{\mathrm{MR}}\right), \tag{1}$$

where r is the radius, E is the allotted energy budget, MR is the flying metabolic rate (for either flapping or soaring flight), and V is the airspeed, with the bird responding to sinking air by increasing MR and responding to rising air by increasing V. The true scenario is more complex, with birds maintaining position within updrafts to gain altitude; however, numerical solution of this strategy requires a fully three-dimensional quantification of the airflow vectors, which is a complex procedure that would produce a similar outcome. The resulting IEPs provide a clear visualization of spatial patterns in the costs of movement, which largely reflect slope angle but are also influenced by local variation in wind vectors (fig. 5).

The construction of IEPs provides substantial advantages over simply mapping an environmental feature in terms of the energetic costs of traversing it (e.g., inclines and the cost of ascent). First, IEPs allow the simultaneous visualization of multiple parameters, summarizing spatial variation in movement costs and travel distance. The IEPs can also quantify spatial variation in movement costs as a function of multiple environmental variables (e.g., incline and substrate) if such variables are known (see also Bohrer et al. 2011, where the distribution of updrafts was modeled using atmospheric and topographic data sets). These can be compared across species, with the energetic allocation given as multiples of RMR. Most importantly, IEPs are directional, and therefore overlaying IEPs on conventional maps will highlight least-cost movement pathways (fig. 5). These can be identified visually or estimated mathematically using a shortest-path algorithm, such as Dijkstra's algorithm (Dijkstra 1959; Rees 2004; LaRue and Nielsen 2008). Although the criteria used by mathematical approaches to rank routes are not always clear, optimal routes could be verified, investigated, and visualized by plotting them over IEPs. Similarly, encoding information about the area and directionality of IEPs would allow the costs of actual pathways (e.g., from animal-borne GPS units) to be estimated and compared with the costs of other available paths. This provides a framework for assessing the cumulative energy savings available through the use of particular environmental features and, ultimately, the role of the energy landscape in route choice.

The final step in this type of approach would be to use a shortest-path algorithm to estimate optimal routes through landscapes defined by multiple resource layers, such as the cost of movement, different attractors (e.g., food resources and the availability of potential mates), and stressors (e.g., the distribution of predation risk and territorial conspecifics). However, this requires knowledge of, assumptions about, or experimentation with the weighting of the various resource layers.

In a static landscape, low-energy routes can, in principle, be learned through experimentation, either by the same animal making many trials or by many animals trying different routes and learning from one another. A single animal may not have the opportunity to experiment, however, in which case it may use an algorithm to move through the energy landscape. The information available to the animal is likely to be incomplete and local (Abrahams 1986), which arises because the animal cannot determine the energy landscape beyond a certain distance, which we term the "perception radius," set by the line of sight or ability to detect other factors, such as temperature, humidity, or flow characteristics. Limitations may also arise from an inability to process large amounts of information quickly. If the energy landscape is only dependent on route, this would provide an objective criterion against which to compare actual paths chosen by animals with incomplete information about the energy landscape.

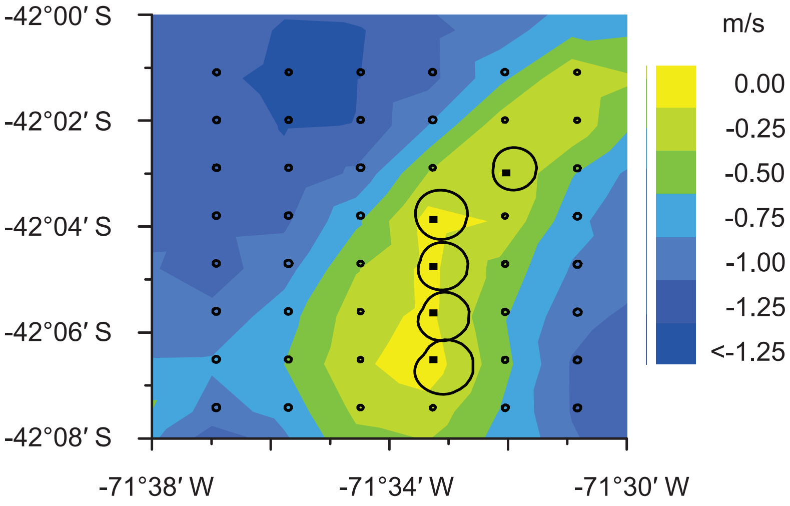

Figure 5: Isoenergy polygons (IEPs) for a black vulture. Airflow was modeled around a simple feature in the foothills of the Andes for an area similar to the home range of black vultures (DeVault et al. 2004). Colored contours indicate the predicted vertical velocity of the air less the sink rate of a gliding black vulture. IEPs represent the distance a black vulture could travel from each starting location (evident in the larger IEPs as filled black squares) with the energy used during 1 min at resting metabolic rate.

Expectations for General Animal Movement Strategies in Energy Landscapes

The above work demonstrates that animals react to the variation in energy expenditure required to move through varying landscapes, yielding a number of specific predictions. First, the critical nature of the relationship between power use and speed, which is essentially linear in terrestrial movement and a power function for swimming animals and powered fliers (for speeds greater than the minimum power speed; Tucker 1970), points to a fundamental difference in the extent of path deviations that are expected from these animals, compared with walkers (fig. 2). In essence, deviations to avoid fluid flow–opposing motion should become disproportionately greater with linear increases in fluid speed (although animals also vary in their ability to increase speed beyond $\mathrm{COT}_{\mathrm{min}}$; Pennycuick 1969). We note here that, even though the power costs of gliding flight increase as a linear function of flight speed (Duerr et al. 2012), soaring animals are also expected to be sensitive to headwinds because of the exponential increase in height loss with airspeed (Pennycuick 2008).

Second, in a general sense, assuming that animals intend to move to a goal minimizing energy expenditure rather than time, animals should favor the route of $\mathrm{COT}_{\mathrm{min}}$ (Rees 2004; fig. 2). We note that animals may deviate either to circumnavigate an area associated with higher costs of movement or to exploit conditions associated with energy savings (Gonzalez-Solis et al. 2009; fig. 3). The higher the costs of the shortest route, the longer may be the alternative, although the difference between these two routes is diminished as the costs of travel approach resting metabolic rate (fig. 2). Thus, animals that move efficiently or those that have high resting metabolic rates, compared with travel costs (Taylor et al. 1972), are expected to deviate least with varying energy landscapes.

Third, the relative temporal invariance of the static energy landscape (table 1) means that animals minimizing COT should move in predictable ways, with low-cost options becoming well-used pathways. Analysis of possible routes to mountain summits has shown that human paths generally do not follow the least-time route but instead minimize the metabolic costs (Rees 2004). Route selection is particularly pertinent for humans moving in mountain terrain, because the COT is sensitive to topography (Minetti et al. 2002). In fact, the greater the variability in the energy landscape, the more regularly “low energy” pathways should be used and the more conserved they should become. Thus, the propensity to follow low-cost paths may vary with habitat type and with season, such that ground-moving mammals should show more bias to low-cost paths in the season in which vegetation is highest, with bias reducing when the vegetative superstrate dies back.

Conversely, fluid environments, particularly air, show considerable temporal variability in the energy landscape (fig. 3), so that route selection as well as the timing of movement by flying animals is likely to be much more variable than that shown by terrestrial animals. Indeed, there is evidence that large soaring birds select different types of updrafts according to environmental conditions, which has implications for route selection (Duerr et al. 2012).

Through the repeated use of particular routes, terrestrial animals may even modify the energy landscape, creating trails with reduced COT through a more compacted substrate or reduced superstrate (Murray and Boutin 1991). Humans have modified the environment extensively to reduce the costs of movement through the construction of road networks and steps, for example, and animals, too, may actively maintain or even engineer aspects of their environment in an analogous fashion. The energetic advantages of this have yet to be examined directly, although the use and maintenance of trails by social insects, such as leaf-cutting ants, can lead to a 4- to 10-fold reduction in travel time to previously discovered resources (Rockwood and Hubbell 1987). Some aspects of trail architecture are even consistent with principles to increase travel speeds (Farji-Brener et al. 2012).

Some of the greatest savings in movement energy will occur when particular locomotion options allow animals to negotiate what is otherwise an impenetrable object, such as a cliff or a body of water (Chevallier et al. 2010). One of the selection pressures for flight illustrates this well and shows the dangers of comparing COT for animals moving through idealized landscapes in or on different media at a constant height. Although flight power costs are higher than those for terrestrial locomotion (Tucker 1970), a glide from one mountain to another can result in much lower COT, particularly if the equivalent terrestrial track involves considerable time and variation in potential energy (Dial 2003; Thorpe et al. 2007). Indeed, any landscape-associated increases in terrestrial locomotion costs would enhance the relative energetic advantages of flight (Dudley et al. 2007).

Finally, if animals are to maximize net energy gain during foraging, they should either avoid costly areas in their energy landscapes or move in a straight line across them, all other factors being equal. This illustrates a direct link between the energy landscape and properties of the movement path (Shepard et al. 2011), including the distribution of step lengths.

Ultimately, of course, the costs of movement in animals can be offset by the form of other distributions, including food, mates, and risk, or can be modulated by other physical parameters, such as temperature, or by the animal’s physiological state. If an animal seems to be moving with little regard for the energy landscape when the predicted variance in the energy landscape is high, this may help inform researchers of the likely importance of other factors, which may be hard to quantify directly.

Expected Second-Order Phenomena Resulting from Energy Landscapes

Energy landscapes are likely to have a profound influence on animal biology beyond the direct effect of movement. This is because energy landscapes contribute to area quality, affecting the areas selected by animals (e.g., for feeding and reproduction) and causing nonrandom movement between them.

In the first instance, we would predict energetically favorable sites to be generally selected by animals, all other factors being equal (Weimerskirch et al. 2012; Wilson et al. 2012). Thus, the energy landscape could help to predict area occupation densities (Wilson et al. 2012) and species range and distribution. For instance, wind energy affects the foraging range and efficiency of soaring seabirds (Furness and Bryant 1996; Weimerskirch et al. 2012) as well as patterns of species diversity at regional scales (Davies et al. 2009). For territorial animals, the energy landscape may also explain patterns of territoriality and dominance; for instance, some fish defend sites on the lee side of rocks, associated with reduced flow (Heggenes 2002), although this may also reflect associated patterns in food availability. This, in turn, has implications for the distribution of predator pressure, with less costly sites potentially becoming associated with reduced prey density as a result. In the case of the red kite searching on the windward or leeward side of the mountain (see above), with air moving at 1 m/s up or down, respectively, rates of prey acquisition would need to be 3.6 times higher on the leeward side to make both sides equally profitable.

The variability in some energy landscapes through time can be compared to the temporal variability in energy derived from food resources (Shepard et al. 2011), and so both may shape life-history strategies in a similar manner. For example, it is generally accepted that seasonal breeding patterns are linked to resource availability (Alerstam 1993), but seasonal availability of updrafts has been proposed to be a major driver for breeding in griffon vultures *Gyps fulvus* (Nathan et al. 2012). Indeed, the complexity of moving through aerial energy landscapes, which are characterized by high variability from hourly to seasonal scales, may explain why juveniles of some vulture species remain with their parents for so long.

The energy landscape can affect not only where and when individuals and populations occur, but also the reproductive success in those areas and patterns of gene flow between them. For instance, a long-term increase in the foraging efficiency of wandering albatrosses *Diomedea exulans*, attributed to a decadal-scale increase in wind intensity, was suggested to be responsible for an increase in reproductive success (Weimerskirch et al. 2012). It is conceivable that a more heterogeneous energy landscape could lead to spatial patterns in reproductive success, influencing whether populations act as sources or sinks, as well as patterns of connectivity between them. For example, consistent landscape factors were found to influence both path selection and genetic differentiation in American black bears *Ursus americanus* (Cushman and Lewis 2010), and there is evidence that oceanic currents influence patterns of dispersal in diverse marine organisms (Monzón-Argüello et al. 2010).

In conclusion, although a number of authors have demonstrated the importance of energy landscapes for modulating animal movement under particular conditions, the general acceptance of the extent to which energy landscapes can influence various fundamental aspects of movement (e.g., speed, timing, and tortuosity) over almost all spatial and temporal scales is poorly appreciated. A more thorough integration of these concepts in future work may help to interpret the complexity of animal movement as well as explore the role of variable movement costs on wider ecological processes. We suggest that environmentally variable COT values could be used in combination with geographic information systems to provide mechanistic values for the resistivity of landscape types to animal locomotion (Sawyer et al. 2011). Although this type of approach is used frequently in landscape ecology (LaRue and Nielsen 2008), metabolic costs have yet to be used as the basis for resistivity metrics. Incorporation of these costs should provide insight into the value of landscapes for animals of conservation concern; for instance, the creation of low-cost movement options can enhance fecundity, as demonstrated in studies using man-made corridors for fish migrating upstream to spawn (Kinnison et al. 2003). Although the link between the energy landscape and the population viability is not always this striking, animals of conservation concern are, by the very nature of being subject to environmental stresses, likely to be among those for whom judicious energy expenditure is most critical for survival.

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APPENDIX A

Role of Energy Landscapes in Structuring Route Selection

Considering the case in which route α necessitates the same cost as a shorter but more energetically onerous route β, the role played by the travel costs with respect to those attributable to resting metabolic rate (simplified to equal those of travel at 0 m/s) is

$$(E_0 + E_\alpha)\, T_\alpha = (E_0 + E_\beta)\, T_\beta, \tag{A1}$$

where E_0 is the metabolic rate at a speed of 0 m/s, E is the power use for traveling (above E_0) for routes α and β, and T is the time spent traveling routes α and β. Rearranging this gives

$$T_\alpha = \frac{T_\beta(E_0 + E_\beta)}{(E_0 + E_\alpha)} \tag{A2}$$

or

$$\frac{T_\alpha}{T_\beta} = \frac{E_0 + E_\beta}{E_0 + E_\alpha}. \tag{A3}$$

Note that the scenario expressed above assumes constant travel speed if time spent traveling is to be converted into distance. The equation can be converted into distance and speed derivatives by substituting T for D/S, where S = speed, and because energy expenditure is a known function of speed for any energy landscape described by $E_\alpha = f_\alpha(S)$ and $E_\beta = f_\beta(S)$, then

$$\left(\frac{D_\alpha/S_\alpha}{D_\beta/S_\beta}\right) = \frac{E_0 + f_\beta(S)}{E_0 + f_\alpha(S)}. \tag{A4}$$

APPENDIX B

Development of a Cost Function for Terrestrial Movement in Topographically Variable Terrain

The form of the energy landscape will vary according to the nature of the environment and the individual behavioral response to it. In general, the COT over a small step will depend on the length of the step (and perhaps also on its direction) as well as the speed. The nature of these functional dependencies is likely to vary with position. This can be developed mathematically rather generally if we express the rate of energy expenditure (the power, or power per unit mass) as some function of vector position $\mathbf{r}$ and vector velocity $\dot{\mathbf{r}}$, such as

$$p(\mathbf{r}, \dot{\mathbf{r}}). \tag{B1}$$

The vector $\mathbf{r}$ is, in general, specified in three spatial dimensions, but if, for simplicity, the animal is confined to the Earth's surface, it is more convenient to use two dimensions for $\mathbf{r}$, the third dimension (height) being considered as a dependent spatial variable. This version of the mathematical framework can be illustrated by placing a specific COT model within it.

First, we suppose that the energy cost of walking is some function f (m, v) of the slope (incline) m and the speed v, as represented by figure 1*A*. The speed v is simply given by the modulus of the velocity vector

$$v = |\dot{\mathbf{r}}|. \tag{B2}$$

The slope of the path can be obtained by taking the (two-dimensional) vector gradient of the surface height $h(\mathbf{r})$, that is,

$$\nabla h \equiv \left(\frac{\partial h}{\partial x}, \frac{\partial h}{\partial y}\right), \tag{B3}$$

where $\mathbf{r}$ is expressed in Cartesian coordinates (x, y). The slope of the path is obtained by taking the scalar product of (3) with the unit vector in the direction of motion:

$$m = \nabla h \cdot \hat{\mathbf{r}}. \tag{B4}$$

The cost function in equation (1) can thus be written as

$$p(\mathbf{r}, \dot{\mathbf{r}}) = \mathrm{f}(\nabla h \cdot \dot{\mathbf{r}}, |\dot{\mathbf{r}}|). \tag{B5}$$

All the terms that appear in the argument of the function f depend on the position $\mathbf{r}$, the velocity $\dot{\mathbf{r}}$, or both.

The energy model can be more complicated by adding terms to represent the costs due to substrate and superstrate. In each case, the additional energy cost can be modeled as being proportional to the distance traveled, so that the increased rate of energy expenditure is proportional to the speed of travel. Thus the cost function in equation (1) can be written as

$$p(\mathbf{r}, \dot{\mathbf{r}}) = f(\nabla h \cdot \hat{\mathbf{r}}, |\dot{\mathbf{r}}|) + k|\dot{\mathbf{r}}|, \tag{B6}$$

where the value of k will, in general, depend on the position $\mathbf{r}$. Again, all the terms on the right-hand side of the equation depend on the position $\mathbf{r}$, the velocity $\dot{\mathbf{r}}$, or both.

The specific cost model developed in equation (6) is not the only possible option that conforms to the general formulation of equation (1), but it illustrates the flexibility of the formulation and shows how a number of layers of information can be combined into a single model. There is, however, one important possible simplification of models of this type. If the animal travels at the speed that minimizes its cost of travel for a particular route, the speed is determined by the landscape, and so the only decisions relate to the choice of route. The energy cost of moving between two points in the landscape will depend only on the locations of those two points. In this case, it is possible to find the minimum possible cost route between any two points in the landscape using Dijkstra's (1959) algorithm. An example of this approach is given by Rees (2004).

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Andean condors *Vultur gryphus* in flight. Photograph by Gonzalo Ignazi.