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What can knowledge of the energy landscape tell us about animal movement trajectories and space use? A case study with humans.

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Highlights

- Modelled least-cost paths can be highly tortuous, mirroring some animal tracks.
- Least-cost paths are scale-independent.
- Least-cost paths are a vital starting point for animal trajectory analysis.

What can knowledge of the energy landscape tell us about animal movement trajectories and space use? A case study with humans.

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Short running title: "*The energy landscape – trajectories and space use*"

Abstract

Recent work has highlighted that 'energy landscapes' should affect animal movement trajectories although expected patterns are rarely quantified. We developed a model, incorporating speed, substrate, superstrate and terrain slope, to determine minimized movement costs for an energetically well-understood model animal, *Homo sapiens*, negotiating an urban environment, to highlight features that promote increased tortuosity and affect area use. The model showed that high differential travel power costs between adjacent areas, stemming from substantial environmental heterogeneity in the energy landscape, produced the most tortuous least-cost paths across scales. In addition, projected territory size and shape in territorial animals is likely to be affected by the details in the energy landscape. We suggest that cognisance of energy landscapes is important for understanding animal movement patterns and that energetic differences between least cost- and observed pathways might code for, and give an explicit value to, other important landscape-use factors, such as the landscape of fear, food availability or social effects.

Keywords:

Optimal movement, least cost pathways, tortuosity, energy landscape, Iso-Energy Polygons

1. Introduction

The concept of optimality in animal behaviours, manifest particularly by the "optimal foraging" literature, purports that animals should exhibit behaviours to maximize energetic efficiency (Pyke et al. 1977). One important facet of this relates to the costs of movement because travel accounts for such a large proportion of animal energy budgets (e.g. Weibel et al. 2004; Wilson et al. 2008). Much of this can be couched within a "cost of transport" (*COT*) framework, (the *COT* is defined as the energy required to move an animal a unit distance (in either J m^{-1} or J kg^{-1} m^{-1}) Schmidt-Nielsen, 1984) with the minimum cost of transport COT_{min}, being a powerful index for comparisons of energetic costs of locomotion within and between species (Fedak and Seeherman, 1979).

For terrestrial animals, movement costs are greatly affected by the form of the terrain and its characteristics, most notably the slope (e.g. Lachica et al. 1997; Minetti et al. 2002), the substrate (i.e. concrete *versus* mud) (e.g. Dijkman and Lawrence, 1997) and the superstrate (i.e. vegetation cover) (e.g. White and Yousef, 1978) as well as the speed (Taylor et al. 1970). The interaction between these terms has led to the development of the "energy landscape" (Wilson et al. 2012), which gives explicit values to movement costs across defined terrains (Shepard et al. 2013). Optimality in animal behaviours would have it that animals should travel with the lowest cost of transport (COT_{min}) (Taylor et al. 1970), which includes selecting the least cost energy paths through the landscape, all other things being equal (Shepard et al. 2013). While this has been examined in fluid media (see Shepard et al. 2013 for examples), treatment of it is notably absent in terrestrial animals (but see Wall et al. 2006), perhaps due to the difficulties of quantifying the costs of movement over the typically heterogeneous terrestrial terrains. What is clear though, is that terrestrial vertebrates moving from one spot to another defined spot, may deviate substantially from a straight line course (e.g. Matthews (2010).

A particular difficulty in examination of wild animal movement is that many factors other than energetics affect animal paths (Gallagher et al. 2017). Here, animal movement needs to be couched in terms of many other factors that influence path trajectories and space use, including; time (Shepard, E. L et al. 2009), food (McIntyre and Wiens, 1999; Pearce-Duvet et al. 2011), predators (Hodges et al. 2014), mates and social interactions (Strandburg-Peshkin et al. 2017). We suggest, however, that this problem can be turned on its head and that a good starting point for people studying wild animals might be to determine the paths that equate to the most efficient travel for animals in any given environment before examining the extent to which animals deviate from those paths. We propose that such deviations may then be allocated to factors other than the energy landscape. In particular, the exercise of determining least-cost paths should, first, indicate the extent to which terrain might contribute to particular movement patterns such as tortuosity (e.g. Benhamou and Bovet, 1989; Knoppien and Reddingius, 1985; Krebs, 1973). Following this, the energetic difference between least cost- and actual pathways could be nominally allocated to 'other factors', couched in terms of one currency (joules), and thereby enhance our understanding of animal movement (Smouse et al. 2010; Tang and Bennett, 2010).

This study develops a model to examine the cost of an animal moving with oriented paths (ie with a defined end-point) through a given environment, with a view to examining how minimizing movement cost affects the form (e.g. tortuosity) of the movement track. Thus, in the same way as zig-zagging up a slope has been shown to decrease movement costs (Llobera and Sluckin, 2007), our study seeks to demonstrate to wild animal biologists the extent to which least cost paths for animals may deviate from a straight line and thereby show that space use may not be solely attributable to predators and social effects (Hodges et al. 2014, Strandburg-Peshkin et al. 2017). For this, we needed a species for which accurate and extensive data on energetics are available so we selected a human walking in an urban area. Our aims were; (i) to provide a model that combines energy expenditure for movement of humans as a function of slope, velocity and land cover, (ii) to use this to quantify how the energy landscape in a real situation affects the energetics of path selection for movement from one defined point to another (such as an external point to a home, a resting site or a den), (iii) to use this modelling exercise as an example for suggesting the extent to which the features of the energy landscape can affect path tortuosity (notably the differences observed between optimal movement and shortest routes) and (iv) to consider the implications of our results for researchers working on the behaviour and space use of animals in general.

2. Materials and Methods

2.1 Relationship between power costs, cost of transport and terrain

The *COT* is dependent on the power use (metabolic rate), which scales with the velocity and the mass of the animal (Tucker, 1973) and depends on the resting metabolic rate (*RMR* - the cost of non-movement), onto which travel costs are superimposed. For the calculation of *RMR*, we used the Mifflin et al. (1990) equation for its simplicity and few, most relevant, predictors, standardizing our sample animal to be a 75 kg, 175 cm high, 30 year old male (1) (Supplemental Information 1 – Appendix A).

Mass-specific *COT* was given by;

$$C = P_u / (V\,M) \qquad (1)$$

where: C is the cost of transport, P_u is the power use, V the velocity and M the body mass (Tucker, 1973) so that for our animal (human) moving on level ground, the relationship between power and velocity is essentially linear (Supplemental Information 1 – Appendix B, Fig. B1)

To incorporate the aspect of velocity in the modelling process (see below), Tobler's hiking function, which gives speed for COT_{min} for people on slopes (Tobler, 1993), was adopted for its simplicity and for its ability to differentiate on- and off-path travel. The two equations of this function for on- and off-path travel are[1]:

$$V = 6\,e^{-3.5\,|\,s+0.05|} \qquad (2)$$

$$V = 6\,e^{-3.5\,|\,s+0.05|}\ (3/5) \qquad (3)$$

where s is slope in tan (radians), and 'on-path' terrains were considered to be urban and/or dirt paths/areas, while 'off-path' terrains were grassland, sand and woodland (Supplemental Information 1 – Appendix C).

[1] Note that the returned values from the above had to be converted from km h^{-1} to m $s^{-1.}$

To account for slope, we noted that the relationship between the vertical mechanical power necessary to lift or lower the centre of a body's mass (*Wvert*) and slope is almost linear (Ardigò et al. 2003) and follows Minetti et al. (2002) and Ardigò, et al. (2003)

$$W = V\, g \sin(\arctan(s)) \qquad (4)$$

where W is the vertical mechanical power, V is the velocity in $m^{-1}\, s^{-1}$, g the gravitational acceleration (9.81 $m\, s^{-2}$) and s the slope in radians (Supplemental Information 1 – Appendix D). The slope in our study area was defined as the ratio of the vertical with respect to the horizontal change = tan (θ), (where θ is in radians), during movement from one point to the next.

Terrain is an important factor of walking energy expenditure (Lejeune et al. 1998; McArdle et al. 2006; Zamparo et al. 1992) and these effects were incorporated in the model using terrain coefficients (*tcf*), from Richmond et al. (2015) (Supplemental Information 1 – Appendix E, Table E1), which act as a simple multiplicative factor to derived power (see below).

In order to integrate the power costs of terms, we used the equation proposed by Ardigò et al. (2003) (Supplemental Information 1 – Appendix F, Fig. F1) which resulted in a cost of transport (in $J\, kg^{-1}\, m^{-1}$) being given by:

$$C = 1.866\, a\, V^2 - 3.773\, b\, V + c + 4.456 \qquad (5)$$

where C is the cost of transport, V is the velocity in $m\, s^{-1}$, $a = e^{4.911 slope}$, $b = e^{3.416\, slope}$ and $c = (45.72\, slope^2 + 18.90\, slope)$, where slope is radians.

To deal with the effects of the land cover on the energetic costs, the *tcf* was incorporated by multiplying the relevant value with the *COT*.

To include the three dimensional distance (*threeDD* – in m) covered in each movement from point to point, another linear term was used (e.g. Brueckner et al. 1991; Leibel et al. 1995) so that equation (5) was finalized to;

$$E = (C)\ tcf\ 75\ threeDD \qquad (6)$$

where the result *E* is the total energy cost in Joules required to walk a distance *threeDD* on a defined terrain (i.e. grassland, sand) characterized by the coefficient *tcf*, for an individual weighing 75 kg expending *C* (cost of transport).

2.2. Algorithm for the least cost pathway - Dijkstra's algorithm

Dijkstra's algorithm (Dijkstra, 1959) was chosen to calculate least cost paths because it is well-documented and extensively used for a variety of applications (e.g. Zhan, 1997, see Supplemental Information 1 – Appendix G). This algorithm (Dijkstra, 1959) was used to compute both the minimum cost and the shortest paths from any starting location to any destination within the study area.

This approach allowed the creation of; one-step cost grids, cumulative cost grids and terrain coefficient, slope and velocity grids, with the direction of movement being the direction of movement following the minimum cost paths from the source point to a pre-defined destination. For this, we defined a maximum vertical change allowed between adjacent points of 0.8 m, which, in the 1 m resolution grid used (see below) gave a maximum permissible slope of *ca*. 38.65°, beyond which climbing was deemed impossible. This follows work by Giovanelli et al. (2015), who found that treadmill walkers could not maintain their balance at slopes beyond 39.2° (Supplemental Information 1 – Appendix G.1).

2.3. Iso Energy Polygons (IEPs)

The Iso-Energy Polygon (IEP) is defined as a 'polygon around a central point in space having limits set by the distance from that central point that an animal can travel in any one direction for a specific amount of energy' (Shepard et al. 2013). The limits for our IEPs were taken to be defined by the energy used by a human during 8 minutes of RMR (Stiegler and Cunliffe, 2006) (Supplemental Information 1 – Appendix H).

2.4. Tortuosity metrics

Two metrics of tortuosity were calculated. The first represented the maximum deviation that a human adopting the minimum cost path between two points would deviate from a direct path (which sometimes differed from a beeline because insurmountable objects, such as buildings, precluded this). The second was the "straightness index" (SI), which identified the straightness of a path (Batschelet, 1981), defined as the ratio between the total length of the direct path between the starting location and the destination, and the total length of the minimum cost path travelled (Valeix et al. 2010), ranging from close to 0 for a very convoluted path, to 1 for an absolutely straight path (Benhamou, 2004).

2.5 Model inputs and outputs

The model was developed in "Netbeans Integrated Development Environment (IDE) 8.0.2" with **Java** Development Kit (JDK) 1.7 with the resolution of the model being that of the elevation grid/DSM used as an input (1 m). The grid containing the land cover type of each of its points in the study area (Supplemental Information 1 – Appendix G.2) was derived from a Google satellite true colour composite with ~0.15 m. resolution (Supplemental Information 1 – Appendix I).

Model outputs consisted of multiple files linked via the coordinate system from the input elevation grid/DSM, with direction of movement being taken as that necessary to move in a straight line to each relevant adjacent point. These allowed the creation of cumulative cost contour maps, velocity, slope and terrain coefficient maps and minimum cost paths as well as shortest distance paths. Files also produced IEP maps (Supplemental Information 1 – Appendix G.3).

2.6 Study Area

The study area comprised the entire Swansea University Singleton campus and surrounding area. It was chosen because the area is well walked by people, and it has a range of slopes and diversity of land cover. The total area of the study was 6,131,646 m^2 and was dominated by urban, woodland and grassland land cover, occupying areas of 2,490,943, 2,006,258, and 1,039,690 m^2, respectively. The study area consisted of extensive gentle slopes comprising ~77.7 % of the total area.

2.7 Energy expenditure along the shortest and (predicted) minimum cost path: an experiment in humans

Ten young healthy participants (7 men and 3 women, age: 28±4 y, height: 1.76±0.14 m, body mass: 75±12 kg, BMI: 25±4 m/kg^2) took part in a randomised and counterbalanced cross-over experiment to assess the energy cost of the shortest and (predicted) minimum cost paths of one of the modelled routes in figure 1 (point ‘O’ to point ‘D’). The experimental protocol was approved by the departmental ethics committee (approval reference: 2018-068) and all participants provided their written informed consent to participate.

Participants were asked to avoid strenuous exercise on the day of testing, and to avoid caffeine for ~4 hours and fast for ~2 hours prior to testing. Following pre-screening, on attendance at the testing site on the Singleton Campus, participants were fitted with a rubber face mask connected to a portable gas analysis system (Metamax 3B, Cortex) for breath by breath analysis of oxygen consumption (VO_2) and carbon dioxide production (VCO_2). Both the flow sensor and the O_2 and CO_2 analysers were calibrated prior to each test. Participants then completed two short walks between two pre-defined points on the Singleton Campus (see Figure 1: Point 'O' to Point 'D'): once following the path of shortest distance and one following the path with the (predicted) lowest energy cost (Table 1). The order of the walks was randomised (envelope method) and participants rested quietly for at least 10 minutes in between each walk. Participants were allowed to walk at their own defined pace and they were guided along the route by an investigator using GPS. Specifically, a smartphone device with the application "trails" was used to track the participants' location while following the modelled paths, although this introduced some inaccuracies due to errors in the GPS tracking (e.g. see Zandbergen and Barbeau, 2011).

Energy expenditure was calculated from the breath by breath measurements of VO_2 and VCO_2 using stoichiometric equations proposed by Frayn (1982) and subsequently modified by Jeukendrup and Wallis, (2005). The primary end point was the total energy cost of each path (in joules), but the average energy expenditure (joules/min) for each 100 m, the time to complete each path (seconds), and the average walking speed for each path ($m\ s^{-1}$), were also calculated. Comparisons between conditions were analysed using paired sample t-tests in GraphPad Prism 7 for Mac OS X with alpha set at $p<0.05$. Data are presented as mean and standard deviations unless otherwise stated.

3. Results

3.1 Cost factors of movement in the study area

The major factors of cost of movement for the modelled walker across the map (as incorporated in equation (6)) were the velocity, slope, *tcf* and distance travelled. The interaction of these factors together in the model makes it difficult to present just one scenario with one factor isolated. However, an attempt to do so is presented below which illustrates terrains within the study area with costs derived from the travel of a walker from a modelled point (O) to various other points placed radially around it at some distance (points labelled A to H). In the most basic sense, this approach showed how the model indicated that cost increased with velocity, slope steepness and magnitude of *tcf* within the chosen environment. Particular points that stem directly from the modelled terms or their interaction are mentioned below.

The effect of the terrain coefficients was affected by slope and speed: Because *tcf* values of 1.2, 1.5 and 2.1 for light and heavy vegetation terrains as well as sand over level ground, respectively, followed a linear relationship with velocity, when velocity decreased with steeper slopes, the *tcf* increased. This resulted in notably higher energy costs for sloped sand and vegetated areas than for sloped urban and dirt land covers (Supplemental Information 1 – Appendix J, Fig. J1 - see classes VII and VI and Appendix K for starting from location Z).

In agreement with the equations incorporated in the overall model, consideration of the, generally gentle, slopes within the study area (see Appendix J, Fig. S10.2 and Appendix K for starting from location Z) resulted on steeper uphill slopes producing higher *COT* values than steep downhill, which, in turn, produced higher costs than gentle slopes, which explained why gentle slopes were often associated with minimum cost paths (Table 1 and Fig. 4 B). In addition, the modelled velocities resulting from the application of Tobler's hiking function (Supplemental Information 1 – Appendix J, Fig. J3 and H and Appendix K for starting from location Z) and its incorporation in

Dijkstra's algorithm similarly followed the real world situations, where steeper uphill and downhill slopes lead to lower velocities. Finally, as a further result of Tobler's hiking function, on-path walking resulted in higher speed estimates than off-path. Thus, slope and land cover had a combined effect on the velocity results for the mapped area, with appreciable variation in travel velocity, ranging from e.g. 0.26 m s^{-1} in heavy vegetation, especially in the steeper slopes, to speeds exceeding 1.26 m s^{-1}, primarily in urban and dirt areas (Supplemental Information 1 – Appendix G and H). When the route involved walking uphill, the observed relationship between slope, speed and cost resulted in the lowest change of increase in *COT* for speeds between 0.25 and 0.75 m s^{-1}. This was thus identified as the optimum range for uphill walking (Supplemental Information 1 – Appendix F, Fig. F1).

3.2 The energy landscape as a least cost path from a central point and energy contours

In the same way that contour maps are a useful tool for understanding the topography, energy contour maps were constructed for interpreting easy movement trajectories within the energy landscape (Shepard et al. 2013). For movement modelled from location O (Fig. 1 A), the derived energy contours were much more uniformly shaped than movement modelled from location Z (Fig. 1 B). This was primarily due to the first location being surrounded by gentler slopes and less heterogeneous terrain. Other differences between the two scenarios included that, for example, for an energy budget equal to 82.5-92.7 minutes of RMR, a walker starting from location 'Z' could access 13.7% more area (Fig. 1 B) than a walker starting from 'O'. This highlights the key role that the starting location plays in affecting area-specific costs of travel (Supplemental Information 1 – Appendix L, Fig. L1). The derivation of Iso-Energy Polygons (IEPs) showed the directionality of facilitated travel irrespective of start or end points in defined trajectories (Fig. 2), demonstrating how terrains might affect travel directions (Fig. 2 A, B) and the severe effect of impassable features within the landscape. In addition to directionality of facilitated travel, the size of the total area covered by each polygon indicated generally the energetic ease of travel within each polygon., with the smaller IEPs being located in areas of high *tcf*, such as those corresponding to sand (at the bottom right of the map) (Fig. 2 A). Larger polygons also tended to have a much more uniform shape, stemming from the homogeneous nature of the terrain at these points, particularly with regard to the slopes (cf. bottom left of Fig. 2 A). Of particular note are the polygons located within the black rectangle (Fig. 2 A), which extended more to the west and east than north or south due to them being located on north-south sloping terrain (Fig 2 B).

3.3 Tortuosity of modelled paths

Even the gentle slopes of the study area could be an appreciable factor of path tortuosity. Specifically, the minimum cost paths deviated from the shortest paths to capitalise on the gentler slopes as this is expressed by the standard deviations of slopes in each comparison of minimum cost and shortest distance paths (Table 1 and Fig. 3 B). However, the heterogeneity of the land cover also had a critical impact on the straightness of the modelled optimum paths. While the modelled shortest paths moved directly through areas irrespective of their *tcf* (e.g. the shortest distance path O-C in Fig. 3), the optimum paths deviated from the shortest path to capitalize on lower *tcfs* areas (e.g. minimum cost path O-C, Fig. 3 C). The latter led to larger maximum deviations and lower “straightness index” (*SI*) paths (Table 1, see Supplemental Information 1 – Appendix M for starting from location Z).

Because slope and land cover factors increased minimum cost path tortuosity compared to shortest paths, all modelled minimum cost paths had a correspondingly greater maximum deviation and lower *SI* (Table 1). The magnitude of these effects was highlighted by the much lower coefficients of variation and standard deviations of these two factors (*CV* of *tcf* and *SD* of slopes, respectively) compared to the modelled shortest paths (Table 1). In short therefore, all minimum cost paths were longer (by a maximum of ~ 14% - Table 1, paths O-C) and more tortuous than the shortest although their total costs and the mean step costs, as well as their CVs, were much lower (by maxima of ~35%, ~41% and ~ 70%, respectively) (Fig. 3 and Supplemental Information 1 – Appendix N, Fig. N1 for the example of path O-G). The extents to which the optimum paths deviated to capitalize on slope and land cover is are highlighted in figure 1.

3.4 Human energy expenditure on a shortest and (predicted) minimum cost path

Energy expenditure during each walk and the total energy cost of each walk are shown in figure 4. The total energy cost of the shortest path was overall ~13% higher than the predicted minimum cost path (360018±71935 *vs* 314076±47451 joules, $p<0.001$, Fig. 4). Participant average walking speed was quicker during the minimum cost walk (2.50±0.26 *vs* 2.23±0.23 m s^{-1}, $p<0.001$), resulting in a shorter time taken to complete the minimum cost path despite the longer path distance (691±76 *vs* 720±78 secs, $p<0.05$). These results underpin the general validity of our modelled data and highlight the energy efficiency and the ease of walking of the minimum cost path compared to the shortest route, showing similar trends to our modelled predictions. Slight discrepancies between predicted and measured values may be due to tracking inaccuracies (see section 2.7), changes in the land cover of the study area, since the acquisition of the Google Earth satellite imagery used by our model for its estimations and variation in speed choice by the participants (different modelled velocities from those measured have a substantial effect in modelled costs by for example increasing the *tcf*).

4. Discussion

The scientific literature has a number of examples of how energy landscapes affect the movement patterns of animals (e.g. LaRue, and Nielsen, 2008; Wall et al. 2006). These studies tend to focus on movement over large scales (cf. LaRue, and Nielsen, 2008; Rees, 2004) and are rarely explicit in quantifying how movement costs vary according to route (Shepard et al. 2016). Shepard *et al.* (2013) however, point out that animals should be favoured if they adhere to least-cost pathways, even over fine movement scales. Our model demonstrates this for humans, including those walking in a relatively ‘benign’ environment, illustrating how least-cost pathways deviate substantially from shortest course tracks over distances of up to hundreds of metres in trajectories that are just 2 km long but which reduce overall trajectory energy by up to ~ 35% (e.g. minimum path O-E versus shortest distance path O-E). Such differences could be much greater if the environment was different, and notably composed of a mix of relatively flat pathways on cleared, even, hard substrate within a matrix of steep slopes on soft substrate with extensive vegetation because the power-use differences between moving on the two are so disparate. The most important factor, within this, is slope because the functional relationship between COT_{min} and slope (incorporated in the modelling process by the appropriate equations, see Supplemental Information 1 – Appendix F, Fig. F1) involves such high energies for slopes deviating from zero (Llobera and Sluckin, 2007; Margaria, 1938). The effects of substrate (Dijkman and Lawrence, 1997) and superstrate (White and Yousef, 1978) on power costs to travel will generally be superimposed on the *COT*, modifying pathways accordingly and these can be incorporated within a general function equation of;

$$COT_{min} = f(slope)\, f(substrate)\, f(superstrate)\, f(speed)\, f(distance) \qquad (7)$$

Since Dikstra's algorithm (Dijkstra, 1959) to find the optimal path uses both COT_{min} and distance *via*;

$$E = \sum_{i=1}^{n} C_{min(i)}\, D_i \qquad (8)$$

where $C_{min(i)}$ is the minimum cost of transport over the terrain *i*, and D_i is the total distance covered traversing it, resulting in a total cost *E*, this allows us to access conditions for putative track tortuosity according to terrain heterogeneity. Specifically, when the environment is so composed that the *COT* can be grouped according to different areas, the decision to deviate around a given area or move straight through it depends on satisfying;

$$C_{dp} < (100\, L_{sp}) / (L_{dp}) \quad \%, \text{ of } C_{sp} \qquad (9)$$

where C_{dp} and L_{dp} are the cost of transport and the length of the diverted path in metres, respectively, and C_{sp}, L_{sp} the cost of transport and the length of the straight path, respectively (cf. Gallagher et al. 2017). In the particular case that the grouped area is circular (Fig. 5), the required percent of eq. 9 is independent of the radius of the cyclical shape and the length of the paths (2*r and ~ π*r). Specifically, the diverted path around the circle has to have a *COT* less than ~ 64% of the *COT* of the straight path through it to be energetically more efficient. This illustrates the important point that least-cost paths are effectively scale-independent as long as distances considered exceed more than one step length of the animal concerned. In other words, consideration of least cost paths applies to animals moving for periods of seconds or months and scales of metres to thousands of km (e.g. Hein et al. 2012; Johnson et al. 2002) and track tortuosity is predicted to vary accordingly (Benhamou, 2004).

An immediate consequence that cognisance of least cost pathways may help elucidate is in speculations stemming from examining animal speed through the landscape, variously represented by metrics such as tortuosity and first passage time (e.g. Gurarie et al. 2016). These are used for example, in state-space models (Patterson et al. 2008), or other approaches (e.g. Benhamou and Bovet, 1989; Knoppien and Reddingius, 1985; Krebs, 1973), to interpret behaviour as, for example, constituting area-restricted search (e.g. Lode, 2000; Valeix et al. 2010) or being due to the efficiency or inefficiency of an animal's orientation mechanism (Benhamou, 2004). While many conclusions may be true, it would seem appropriate, at least, to ascertain the extent to which the environment is energetically homogeneous for movement, to rule out least-cost path elements in animal trajectories in the same way that ecologists now generally accept the importance of barriers in affecting animal movement (e.g. Beyer et al. 2016).

4.1 Iso-Energy Polygons (IEPs)

The production of IEPs effectively uses the track tortuosity that stems from linear least-cost pathways and projects them into proper 2D space. As such, they indicate enhanced movement paths in any direction for any particular environment. This has more value than simply helping workers to visualise the costs of movement within the landscape (via the size of the IEP – Fig. 2 and the facilitated directions of movement for their study animals (shown by the asymmetry in the IEP – Fig. 2). The IEP represents an energetic 'value' statement for areas used by animals (Wilson et al. 2012). Relatively large IEPs are obviously pertinent to territorial animals (Powell, 2000) since they represent terrains that are easy to cross and thus have reduced movement-based foraging costs (Mitchell and Powell, 2004). This also translates to easy access to peripheral areas, which may facilitate territorial patrol costs, which can be considerable (Carpenter and MacMillen, 1976; Ewald and Carpenter, 1978; Jaeger et al. 1983). In this regard, it would be useful to consider the extent to which territory boundaries reflect, or not, an IEP from the central place; ie that it is equally costly for animals to reach the boundary in any direction from the central place (*sensu* coyote territories Taylor et al. 1970) (cf. Powell, 2000; Whittingtonand et al. 2005; Bevanda et al. 2015). If boundaries are based on IEPs, we should be able to predict territory shape if the energy landscape of the environment is known. If boundaries are not based on IEPs, the differential energy invested in moving to certain high-cost boundaries has implications for allocation of time and energy to defence within heterogeneous landscapes that have other elements of variable value, such as food (see below).

4.2 Comparison of least-cost pathways with observed pathways; factors beyond the energy landscape.

Thus far, our approach has deliberately ignored drivers of animal movement other than energy landscapes, a substantial simplification given that movement patterns depend on a suite of other critical factors, including searching for food (McIntyre and Wiens, 1999) and mates (e.g. Pearce-Duvet et al. 2011), interacting with conspecifics (Strandburg-Peshkin et al. 2017) and avoiding predators (e.g. Hodges et al. 2014). Given that the energetics of movement is expected to play a role in path choice (e.g. Wilson et al. 2015) because movement is a major energy expenditure element in animal lives (e.g. Weibel et al. 2004; Wilson et al. 2008), we propose that a least-cost pathways approach can help us identify and perhaps even quantify other important movement- and space-use drivers.

Because the various movement drivers are couched in diverse ‘currencies’, which makes their relative importance poorly comparable (Atkinson et al. 2002), we suggest that there is merit in calculating least cost pathways for given start and end points in directed trajectories - such as a foraging animal returning to its central place – (cf. Fig. 1) before comparing this to the observed pathway and expressing the difference in joules (Gallagher et al. 2017). The difference may be due to imperfect knowledge of the terrain (Pyke, 1978) or represent the extent to which the animal might benefit by avoiding, or using, a particular area. Thus, for example, an animal using an energetically taxing shortest distance trajectory (cf. shortest path O-C in Fig. 1 and Fig. 3, which uses ~211031 joules more than by following the minimum cost path; and is some 28.5% more costly) might be time-limited, such as in an animal provisioning its young (Shepard et al. 2009). Alternatively, an animal may display a much greater path length than the least-cost path to avoid an area with predators (Hodges et al. 2014). Examples of this include wolves avoiding regions that are well used by humans such as towns, roads and human-used trails (Whittington et al. 2005). In both cases, the difference in energy expended may give some measure of the importance of the factors affecting path choice.

4.3 What is needed to construct least-cost pathways and IEPS?

The approach taken here, to create least-cost pathways and IEPs, requires knowing the functional relationships between power, speed and terrain as well as having accurate digital maps of the area. While the latter is not difficult, the former may be problematic (we explicitly used humans as a model animal because so much is understood about their energetics). We suggest, however, that humans may constitute a good general model to indicate trends because the problems they face in varying energy landscapes are mirrored in essence, if not in degree, by many terrestrial mammals (White and Yousef, 1978). In fact, the metabolic costs of transport for humans are similar to those of other mammals, with the metabolic energy expended by quadrupeds and bipeds – of similar body size – being nearly the same, even with the large differences in locomotion mechanics and morphology (Roberts et al. 1998). The physics of potential energy change, substrate deformation and superstrate resistance is not expected to change this substantially (Shepard et al. 2013). Thus, identification of the heterogeneity of the terrain, even when humans are used as a model species for transport costs, should alert researchers to the extent to which animal tracks and area use may be affected by the energy landscape, something that should be considered before other movement drivers are assumed (see above).

Finally, the least-cost pathway approach should be cognisant of the specific reasons behind animal movement (Nathan et al. 2008). The least-cost approach is most applicable for directed movement towards a defined target, where an animal, such as a wolf, returns to its den. However, it also has application for other movement behaviours such as foraging in soaring raptors or gulls (Chapman et al. 2011; Mellone et al. 2012 Shepard et al. 2016) and may even be used to calculate metrics of 'fitness', for animals, such as some mountain herbivores, which have males that move rapidly up and down slopes, ostensibly as an honest signal of mate quality. We believe that it will be least valuable for pursuit predator/prey interactions, where prey are expected to be moving with close to maximum power (Wilson et al. 2015) although, even here, the vagaries of the terrain may be pivotal in determining capture or escape (Wirsing et al. 2010).

5. Conclusions

This study shows the extent to which terrain can affect track trajectory in a model animal attempting to move with least cost. It indicates that an environment that incorporates features that necessitate highly variable movement costs will have least cost pathways incorporating increased track tortuosity, with tortuosity scaling according to the size of variable terrain patchiness and barriers. Beyond this, we expect the niceties of energy landscapes to elicit preferred directionality in travelling animals and suggest that, where least cost pathways are not chosen, the energetic cost difference between the least-cost and observed pathways may be indicative of the extent to which factors other than energy landscapes might be affecting movement patterns.

List of abbreviations

C: “Cost of transport”

C_{dp}: “Cost of transport, diverted path”

C_{min}: “Minimum cost of transport”

C_{sp}: “Cost of transport, straight path”

CV: “Coefficient of variation”

DSM: “Digital surface model”

E: “Total energy cost”

Ht: “Height”

IEP: “Iso–energy polygon”

J.: “Joules”

kg.: "Kilograms"

L_{dp}: "Total length diverted path"

L_{sp}: "Total length straight path"

m.: "metre"

M: "Body mass"

Max. dev.: "Maximum deviation"

P_u: "Power use"

RMR: "Resting metabolic rate"

SD: "Standard deviation"

SI: "Straightness index"

tcf: "terrain coefficient"

V: "Velocity"

W_{vert}: "Vertical mechanical power"

Declarations

Availability of data and materials

It is confirmed that the datasets generated in the present study, are available via the Figshare repository and the following links:

https://figshare.com/s/1d733bffa08a01806d7c

https://figshare.com/s/6f9be951f5e755a9843d https://figshare.com/s/9fe7c452064f6f28a6c1

https://figshare.com/s/37bd3d14ec0865df471b

https://figshare.com/s/86b28d95cbee8921f3dd

Ethics approval and consent to participate

There were no participants in the modelling part of this study. The empirical work using participants was approved by the Swansea University's ethics committee.

Competing interests

The authors declare that they have no competing interests and there are no pertinent commercial and other relationships to be characterized as conflicts of interest.

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Figures' captions and tables.

Figure 1. Colour-coding for the cumulative costs of traversing the landscape. *(A) from starting location O and (B) from starting location Z. Costs are represented in minutes of "Resting metabolic rate" (RMR) for a male adult weighing 75 kg weight and measuring 175 cm high. The percentages in each class represent the proportion of the total area accessible for each cost while the different colours in the paths represent the summed distances from different segments of 350 m. length. Each source to destination trajectory shows two options; the coloured is the least-cost path while the grey is the shortest path between insurmountable objects (for definitions see text).*

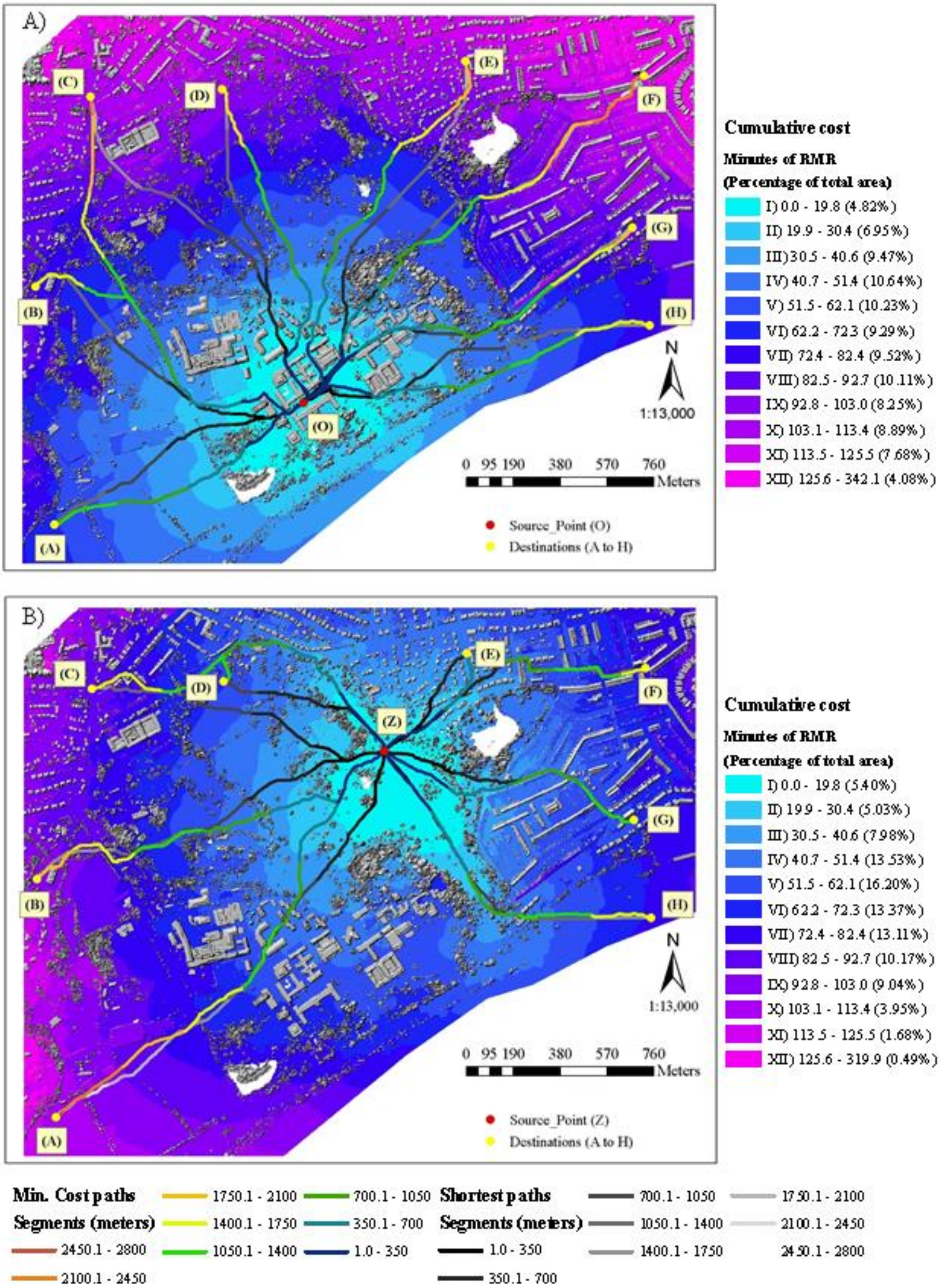


Figure 2. The "Iso-Energy Polygons" (IEPs) in the study area. *(A) Derived for equally spaced points across the map. Different colours represent different polygons, while the starting location of each polygon is represented by a circle. The size of its*

polygon is limited to the costs that would be incurred for 8 minutes of "Resting metabolic rate" (RMR), for a male adult weighing 75 kg and 175 cm height. (B) Expanded view of the inset represented by the black rectangle area over a slope of the terrain. Arrows indicate favourable directions of movement.

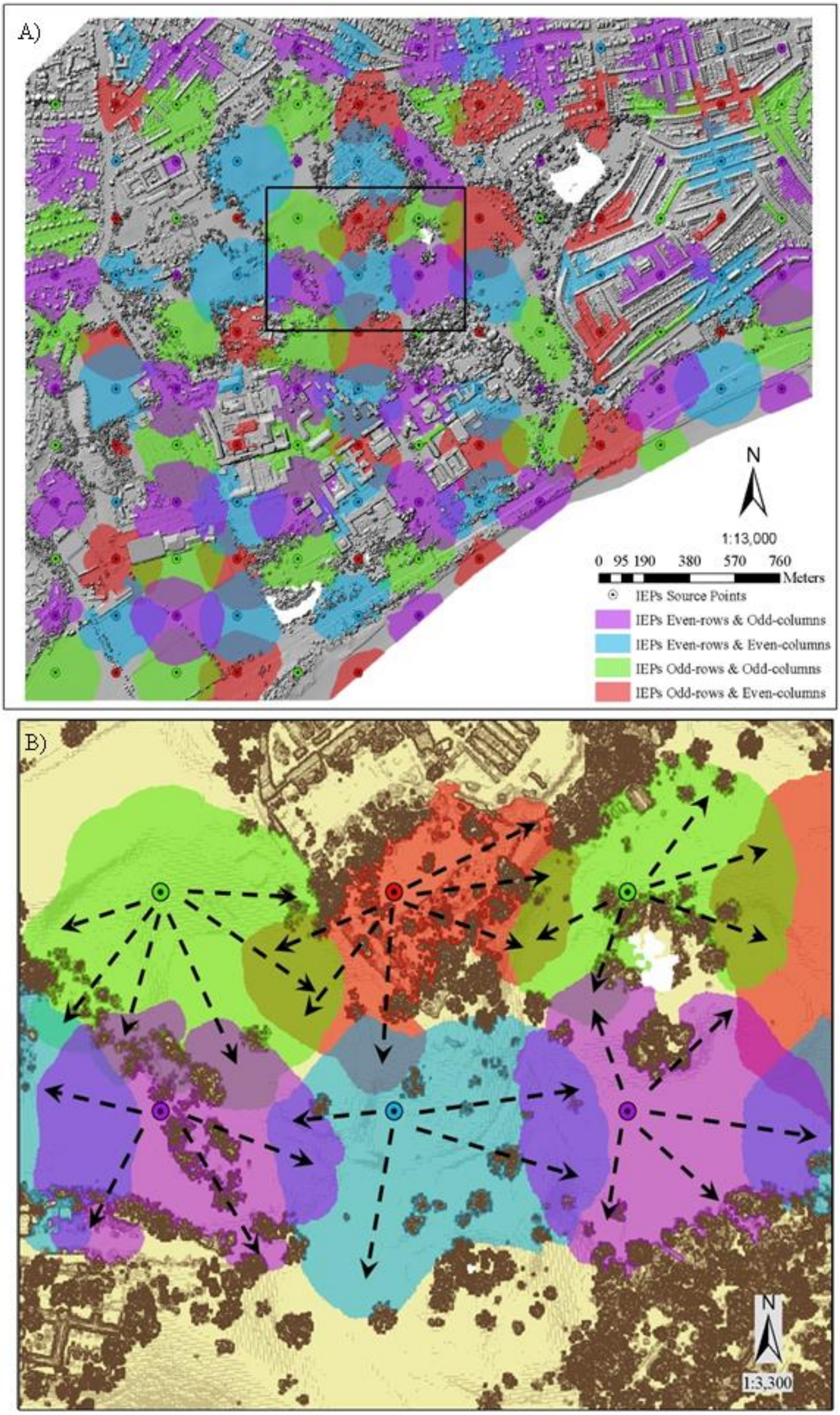

A)
N
1:13,000
0 95 190 380 570 760
Meters
IEPs Source Points
IEPs Even-rows & Odd-columns
IEPs Even-rows & Even-columns
IEPs Odd-rows & Odd-columns
IEPs Odd-rows & Even-columns
B)
N
1:3,300

Figure 3. Minimum cost (orange line) and shortest distance paths (grey line) for the trajectory O-C against distance travelled. *The black line represented the "general additive model" (GAM) fit in the data for the shortest, and the orange-red line the GAM fit for the minimum cost. (A) shows the costs between adjacent cells in the paths, (+- ½ SD), (B) shows the slopes between adjacent cells in the paths, (+- 1 SD), (C) shows the terrain coefficients walked in the paths (+- ½ SD) while (D) shows the velocities resulting from the application of Tobler's hiking function in the paths, (+- ¼ SD). The coloured and the black-grey-white bars, indicate the appropriate segments of 350 m. length each, in the minimum and shortest paths, respectively, in Fig. 1.*

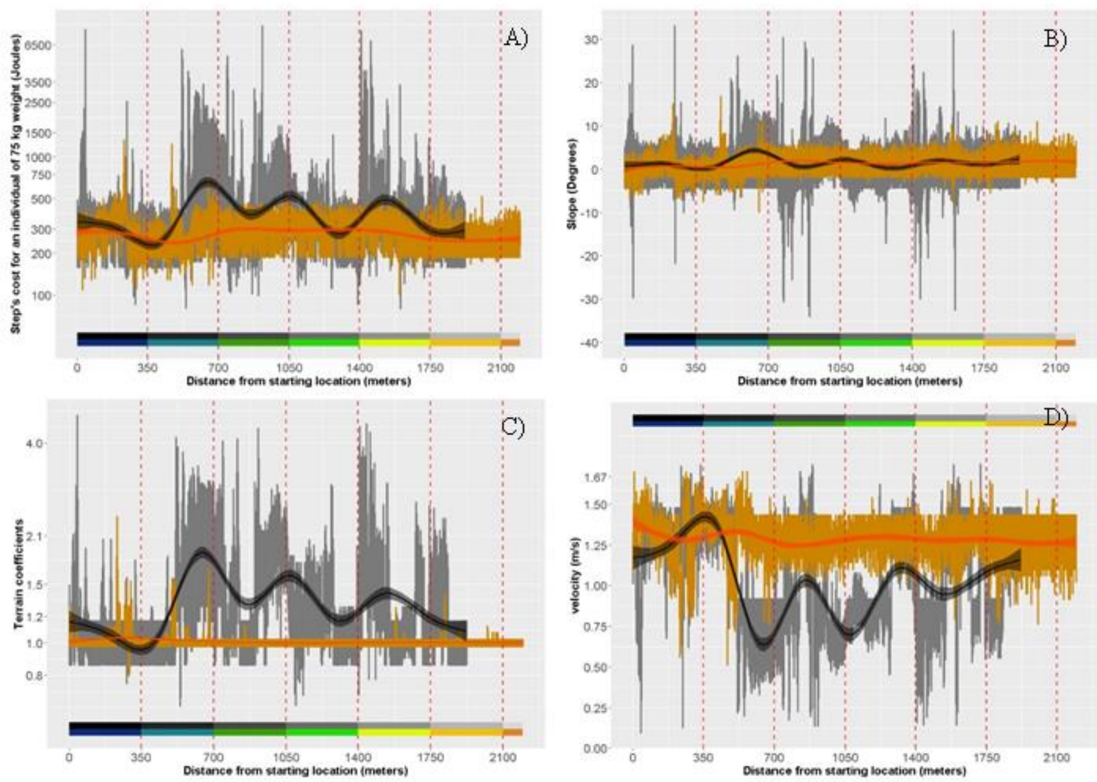


Figure 4. Movement energy expenditure (j/min) of walking along the shortest (solid line) and predicted minimum cost (dotted line) paths (A) and the total energy cost of walking each path (B). *Data are presented for n=10 human participants walking from point 'O' to point 'D' shown in figure 1A. Data are shown as mean and standard deviation in figure 4A, and mean (open bars) and individual data points (lines) in figure 4B. * denotes p<0.001 for difference in energy cost of walking the shortest compared with the minimum cost path.*

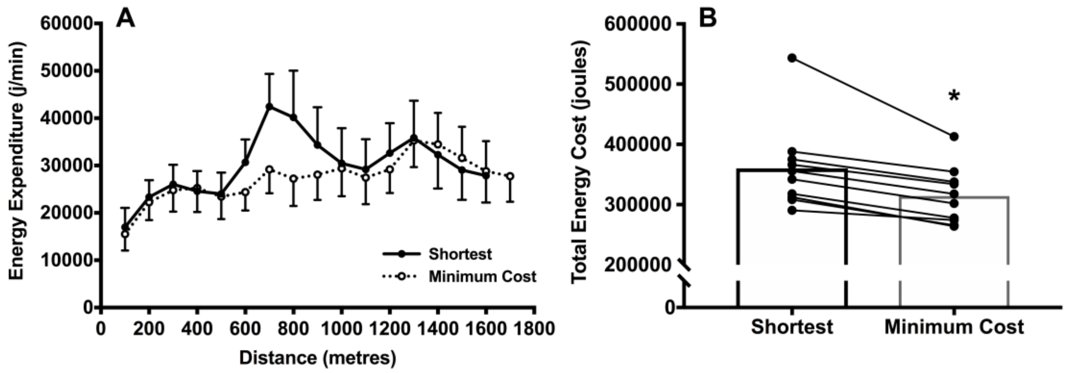
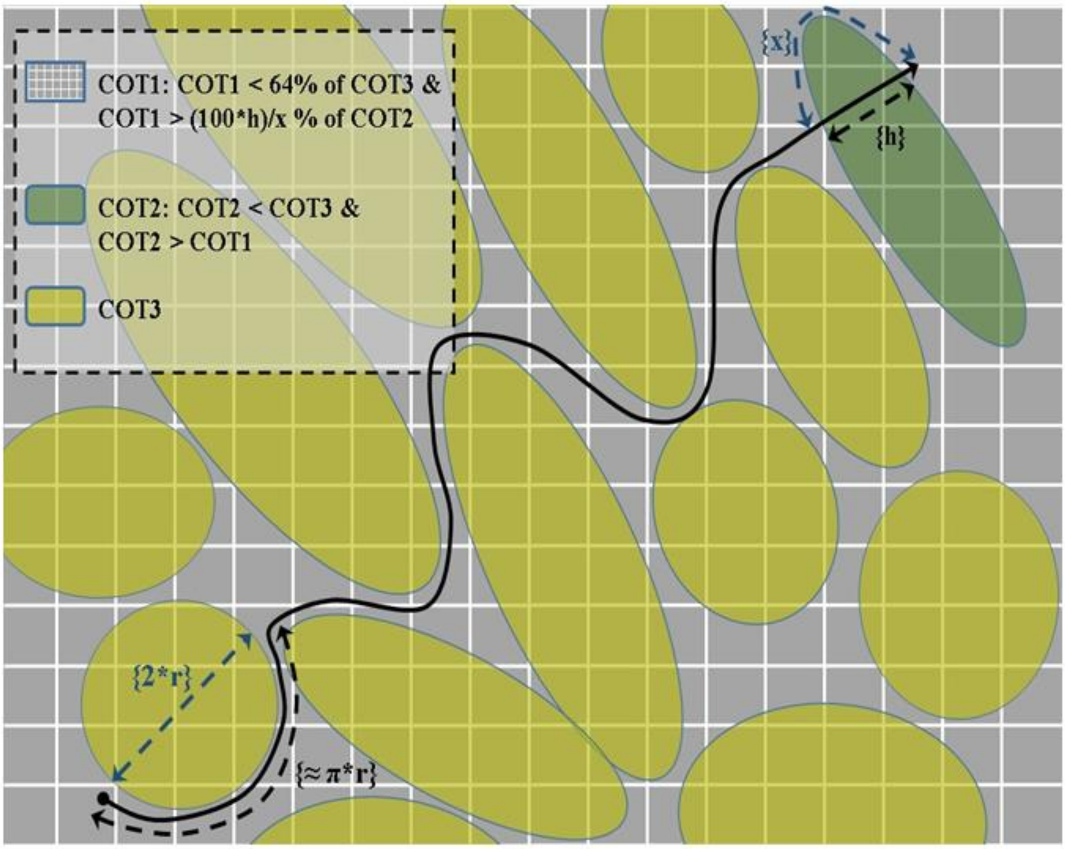


Figure 5. Optimal movement in hypothetical terrains. *Optimal movement (for energy) on a heterogeneous terrain with three different groups of cost of transport. Grey squares, indicate low energy-cost (COT1 e.g. 6 J kg^{-1} m^{-1}), the green oval shows medium energy-cost (COT2 e.g. 10 J kg^{-1} m^{-1}) and olive areas show high energy-cost (COT3 e.g. 50 J kg^{-1} m^{-1}). The black line represents the optimal route and black dashed lines indicate the length of the first and last segments of this route, π*r and h, respectively. The blue dashed lines indicate two alternative routes of these two segments*

*with length 2*r (diameter) and x, respectively, with r, the radius of the area shown in the bottom left. Note that these conditions are scale independent, i.e. apply whether the grid squares have sides of length 1 m or 100 km.*



Paths	*Total cost (Joules)*	*Total distance (metres)*	*Mean COT ($J\ m^{-1}$)*	*CV of steps' cost (%)*	*CV of velocity (%)*	*CV of terrain coefficients (%)*	*SD of slopes*	*Mean of step cost (J)*	*Mean of velocity ($m\ s^{-1}$)*	*Mean of terrain coefficients*	*Mean of slopes (°)*	*Straightness index*	*Maximum deviation (metres)*
O-A min. path	311675	1383.6	225.3	37.5	25.2	14.5	2.2	267.3	1.13	1.1	-0.19	0.89	118
O-A shortest path	381887	1345.4	283.8	162.3	27.0	34.2	3.9	342.8	1.15	1.18	-0.17	0.92	100.91
O-B minPath	402632	1678.8	239.8	33.5	18.9	15.0	2.3	287.2	1.21	1.06	0.66	0.77	198.04
O-B shortPath	506661	1571	322.5	132.5	27.8	34.3	3.9	398	1.11	1.23	0.72	0.83	205.4
O-C minPath	525291	2194.4	239.4	26.9	11.2	6.3	1.9	279.3	1.28	1	1.25	0.76	416.99
O-C shortPath	736323	1922.2	383.0	110.8	31.2	37.2	4.3	466.3	1.03	1.34	1.43	0.86	180.97
O-D minPath	514060	1715.2	299.7	49.8	26.7	23.4	2.2	361.8	1.06	1.21	1.51	0.84	151.34
O-D shortPath	653557	1587.7	411.6	117.4	32.9	34.8	3.7	464.8	0.93	1.44	1.65	0.91	77.45
O-E minPath	533564	2053	259.9	56.6	22.0	21	3	313.9	1.12	1.12	0.81	0.82	177.85
O-E shortPath	817300	1876.8	435.5	190	32.3	40.5	5.6	532.1	0.95	1.41	0.93	0.90	102.55
O-F minPath	612921	2480.4	247.1	72.9	19.7	21.1	2.5	299.3	1.21	1.1	0.46	0.85	173.51
O-F shortPath	829633	2385.4	347.8	177.0	28.4	38.3	5.0	434.1	1.11	1.25	0.49	0.88	172.08
O-G minPath	428320	1880.2	227.8	37.4	18.7	15.6	2.7	283.5	1.24	1.05	0.06	0.88	112.19
O-G shortPath	523703	1826.6	286.7	127.7	25.4	32	3.9	354.8	1.14	1.2	0.06	0.91	112.94
O-H minPath	388866	1773.1	219.3	28.6	15.9	21.8	2.2	250.9	1.29	1.07	-0.34	0.89	97.17
O-H shortPath	508998	1733.9	293.6	125.5	27.5	45.1	3.5	326.3	1.05	1.34	-0.33	0.91	82.4

Table 1. Data describing the shortest and minimum cost paths from the starting location 'O' to various destinations. *From left to right: Total cost in Joules, Total length of each path in metres, mean cost of transport calculated as total cost/total length, "Coefficient of variation" (CV) of costs between adjacent cells in the paths, CV of velocities resulting from the application of Tobler's hiking function between adjacent cells in the paths, CV of terrain coefficients walked in the paths and "Standard deviation" (SD) of slopes between adjacent cells in the paths. The means of each feature follow in the same order. Finally, the "straightness index" (SI) and "Maximum deviation" (Max. dev.) from the shortest paths, represent the tortuosity of each path. (see Supplemental Information, Appendix L for the data analysis of the paths starting from location Z)*