SHORT COMMUNICATION

A different angle: comparative analyses of whole-animal transport costs when running uphill

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ABSTRACT

Comparative work on the cost of terrestrial locomotion in animals has focused on the underpinning physiology and biomechanics. Often, much of an animal's energy budget is spent on moving around; thus, there is also value in interpreting such data from an ecological perspective. When animals move through their environment, they encounter topographical variation, and this is a key factor that can dramatically affect their energy expenditure. We collated published data on the costs for birds and mammals to locomote terrestrially on inclines, and investigated the scaling relationships using a phylogenetically informed approach. We show that smaller animals have a greater mass-specific cost of transport on inclines across the body mass range analysed. We also demonstrate that the increase in cost for smaller animals to run up a slope as opposed to along a flat surface is comparatively low. Heavier animals show larger absolute and relative increases in energy cost to travel uphill. Consideration of all aspects of the cost of incline locomotion – absolute, relative and mass specific – provides a fuller understanding of the interactions between transport costs, body mass, incline gradient and phylogeny, and enables us to consider their ecological implications, which we couch within the context of the 'energy landscape'.

KEY WORDS: Incline running, Phylogenetics, Energy expenditure, Net cost of transport, Metabolic rate

INTRODUCTION

Comparative analyses of the energy expended by animals to locomote have shed light on how their size relates to the cost for them to move around their environment. While in absolute terms the metabolic cost of terrestrial locomotion increases with an animal's size, per unit mass this cost is lower in larger species (Full et al., 1990; Schmidt-Nielsen, 1972; Taylor et al., 1970). However, most of these data have been derived from animals running on the flat, whereas natural environments often encompass sloping ground, which is another factor likely to have a large effect on animals' energy transportation costs. Thus, a better understanding of the energy expended by wild animals when traversing a landscape is gained from measurements of movement costs on different gradients. Recently, several papers have analysed across-species relationships between the net cost of transport (NCOT; ml O_2 m^{-1}), the incline of the ground being walked on and animal body mass.

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Snyder and Carello (2008) provide evidence that the efficiency of animals in converting metabolic energy into vertical work when walking up a slope increases with body mass up to around 1 kg, and both Tullis and Andrus (2011) and Lees et al. (2013) indicate that per unit mass the cost for an animal to move uphill is lower for larger species, again up to a mass of about 1 kg. The interpretation from all of these studies is that the energy disadvantage experienced by particularly small terrestrial animals when walking on the flat is exacerbated on an incline.

However, these previous analyses all considered inter-specific scaling of the cost of transport on a mass-specific basis. Such 'pound for pound' analyses facilitate comparisons between species of greatly varying sizes, and provide a means for determining the mechanisms underlying inter-specific correlations. However, as mass-specific values do not reflect the absolute energy expenditure for an animal, they may also not reflect the ecological consequences to the animal of those metabolic costs.

Furthermore, concern has been raised (Lees et al., 2013) that inherent confounds limit the comparative power of the incline NCOT data available in the literature (Lees et al., 2013; Tullis and Andrus, 2011), and as such the conclusions from these studies have been tentative (Lees et al., 2013; Snyder and Carello, 2008; Tullis and Andrus, 2011). The issue is that, in all these papers, the analyses implicitly or explicitly assume that the relationship between energy expenditure and slope angle is linear and passes through the origin (isometry; Packard and Boardman, 1999). If this assumption does not hold, then comparisons between species measured on non-identical gradients might be misleading, and comparisons of animals of different size would be particularly problematic if there is a confound between animal mass and incline range. These challenges bring into question the robustness of the repeatedly stated conclusion that there is an effect of body mass on the economies of incline locomotion only in smaller animals.

Similarly to previous studies, here we examined the effect of body size on the energetics of incline locomotion by compiling data from the literature for species representing a wide range of sizes and analysing the relationships between NCOT, body mass and slope angle. However, our interrogation of the data explicitly includes whole-animal NCOT and relative NCOT as well as mass-specific NCOT, and also incorporates information on phylogenetic relatedness. We focus on birds and mammals alone, for which the range of inclines employed overlap well and previous studies have shown no systematic difference in NCOT (White et al., 2016). We establish that across the species included there is no evidence for systematic non-linearity in the (non-transformed) relationship between NCOT and gradient, at least for the non-negative gradients for which most published data are available. By investigating variability in the mass scaling exponents of the slopes between NCOT and incline gradient, our analyses do not assume isometric relationships between the energy cost to move and gradient angle.

We use these data to demonstrate how considering patterns in all formulations of NCOT – absolute, relative and mass specific – enables interpretation of the findings from an ecological perspective in the context of energy landscapes (Wilson et al., 2011).

MATERIALS AND METHODS

Data for NCOT (ml O_2 m^{-1}) were compiled from peer-reviewed literature, from studies where animals ran at more than one gradient, and were converted to J m^{-1} assuming an energy equivalence of O_2 of 20.1 J ml^{-1}. NCOT was defined as the slope of a linear regression relating metabolic rate and speed of terrestrial locomotion at a fixed incline. In all studies included, the animals always ran directly along the treadmill in a cranial–caudal direction. The speeds and slopes applied were selected by the experimenters. Where NCOT values were not supplied, data were digitised for regression analysis. In total, data were collected and analysed for 24 species, ranging in mass from the 30 g mouse *Mus musculus* to the 492 kg horse *Equus ferus*. Mass values for each species were compiled from the same studies from which NCOT data were compiled. Although data were available in the literature for many groups of animals locomoting on inclines up to 90 deg, we limited the analysis to birds and mammals on inclines less than 90 deg to ensure that there was no association between body mass and incline in the data set (the largest incline in the data set was 37 deg, and we excluded one measurement of NCOT for humans climbing up a vertical wall; Booth et al., 1999). For each data set, we calculated the slope of the relationship between NCOT (J m^{-1}) or mass-specific NCOT ($NCOT_{ms}$; J kg^{-1} m^{-1}) and gradient (deg) using linear regression. For data sets where animals were measured running on the level (0 deg; all but three data sets), we also calculated relative NCOT ($NCOT_{rel}$) by dividing all NCOT values by the value of NCOT measured at 0 deg, and then calculated the slope of the line relating $NCOT_{rel}$ to gradient. For some species, data were available from more than one study, or for more than one cohort of animals. In these cases, each study or cohort was analysed as a separate data set, except for the study of Lees et al. (2013), for which winter and summer animals were pooled (NCOT increased with incline for both winter and summer birds in this study, but the magnitude of the increase was inconsistent with other studies unless the data were pooled). Studies of elk (Cohen et al., 1978), reindeer (Fancy and White, 1987), and mountain goats and bighorn sheep (Dailey and Hobbs, 1989) all provided unique mean mass values for each gradient, and so these were averaged for analysis.

For those data sets that included measurements of NCOT at more than three non-negative gradients (Fig. 1), we tested for non-linearity in the relationship between NCOT and non-negative gradient by testing the significance of a quadratic term in a multiple regression. The quadratic term was significant for quails *Coturnix coturnix* (t_1=−19.1, P=0.03; Fig. 1A) and for the human data set spanning the greatest range of gradients (t_4=17.2, P<0.001; Fig. 1I); the quadratic term was non-significant (P≥0.1) in all other relationships. The relationship for quails appears anomalous, however, because across the full range of (positive and negative) gradients, the relationship exhibits downward curvature for quails and upward curvature for all other species (Fig. 1); for humans, the quadratic explains only 1.6% more variance than the linear function. Although upward curvature appears common in these data, especially for negative gradients, most data sets provide measurements at too few gradients to reliably quantify the curvature (Fig. 1). For the present study, we therefore used linear functions as a reasonable description of the relationship between NCOT and gradient for non-negative gradients.
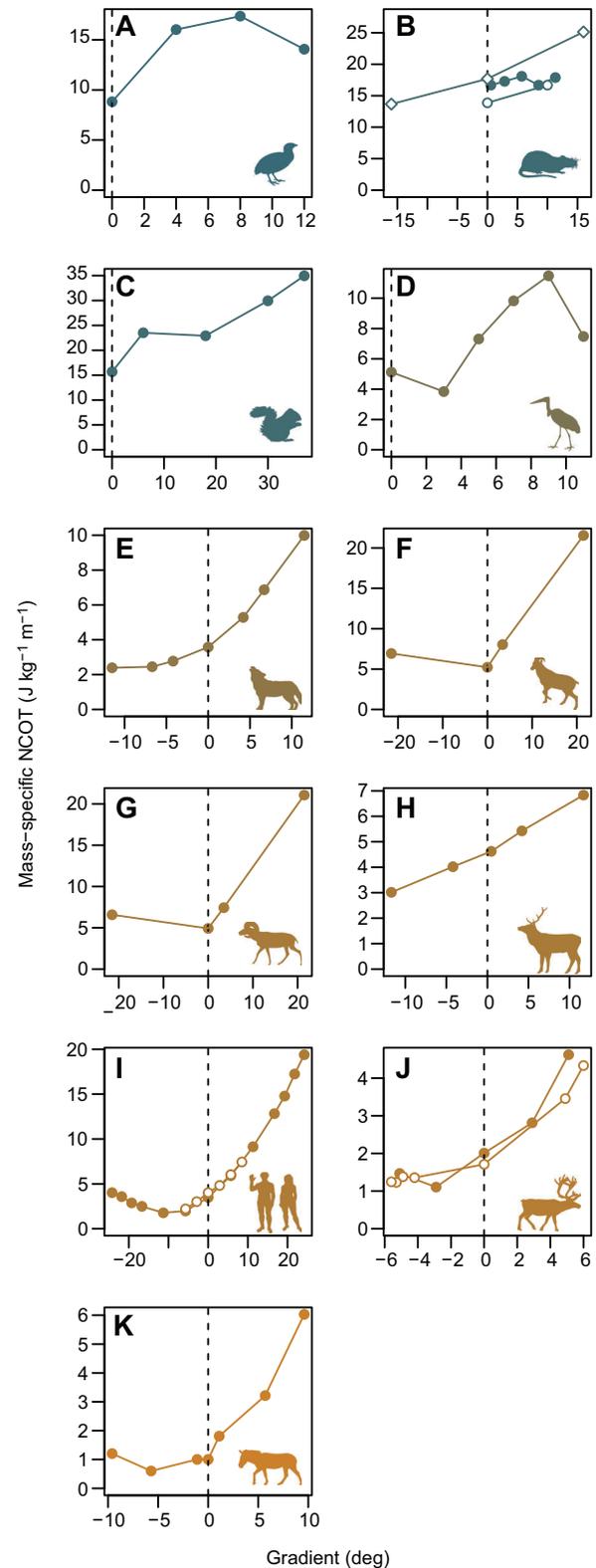

Fig. 1. See next page for figure legend.

Data were analysed using phylogenetic mixed models (Hadfield and Nakagawa, 2010; Housworth et al., 2004; Lynch, 1991) implemented in the ASReml-R (Gilmour et al., 2009) package of R v3.0.2. Phylogenetic mixed models were selected over the more commonly used methods of independent contrasts (Felsenstein,

Fig. 1. The relationship between mass-specific net cost of transport (NCOT) and gradient for different species. NCOT was measured over more than three gradients (irrespective of whether those gradients were negative or non-negative). (A) Common quail *Coturnix coturnix*, (B) brown rat *Rattus norvegicus* (filled circles: 0.20 kg, open circles: 0.22 kg, open diamonds: 0.30 kg), (C) pine squirrel *Tamiasciurus hudsonicus*, (D) maribou stork *Leptoptilos crumeniferus*, (E) dog *Canis lupus*, (F) mountain goat *Oreamnos americanus*, (G) bighorn sheep *Ovis canadensis*, (H) elk calves *Cervus canadensis*, (I) human *Homo sapiens* (filled symbols: 61.2 kg; open symbols: 70 kg), (J) caribou *Rangifer tarandus* (filled symbols: 96 kg; open symbols: 102 kg), (K) horse *Equus ferus asinus*. Data and sources are provided in Table S1. Original image for pine squirrel, ©John Plaistow (licensed under CC BY-SA 3.0 https://commons.wikimedia.org/w/index.php?curid=681073). The data are coloured by $\log_{10}$(mass) from lightest species (blue) to heaviest (orange).

1985; Rezende and Diniz-Filho, 2012) and phylogenetic generalised least squares (Grafen, 1989; Rezende and Diniz-Filho, 2012) because phylogenetic mixed models can formally incorporate phylogenetic non-independence as well as non-independence associated with multiple measurements of single species (i.e. multiple studies of the same species). The tree used for analysis was constructed using published trees for mammals (Bininda-Emonds et al., 2007) and birds (Jetz et al., 2012). The mammal tree was constructed using a formal supertree approach to combine published trees estimated by a range of methods (Bininda-Emonds, 2004), and was built using an explicit source tree collection protocol that minimised data duplication and the inclusion of source trees of lesser quality, such as those based on taxonomy. The bird tree was assembled using sequence data for four protein-coding mitochrondrial genes (cytochrome b, 4902 species; cytochrome oxidase I, 2335 species; NADH dehydrogenase subunit 2, 4308 species; and NADH dehydrogenase subunit 3, 1232 species), and six nuclear loci [recombination activating protein 1 (rag-1), 1528 species; beta-fibrinogen intron 5 (bfib5), 1089 species; beta-fibrinogen intron 7 (bfib7), 1460 species; glyceraldehyde 3-phosphate dehydrogenase (gapdh), 967 species; myoglobin (myo), 1867 species; and ornithine decarboxylase (odc), 1405 species], which was combined with taxonomic information for species lacking sequence data to build trees for each of 158 clades that were then grafted onto a backbone phylogeny (Hackett et al., 2008). For birds, we constructed a single majority rule consensus tree from the published posterior distribution of 10,000 trees (Jetz et al., 2012) using 'ape' v3.1-1 (Paradis et al., 2004). For the combined mammal and bird tree, branch lengths were estimated using Grafen's (1989) arbitrary branch length transformation (branch lengths set to a length equal to the number of descendant tips minus one).

The models included $\log_{10}$-transformed data for the slope of NCOT on gradient, the slope of $NCOT_{ms}$ on gradient or the slope of $NCOT_{rel}$ on gradient as the dependent variable, $\log_{10}$(body mass) (where body mass is in kg) as a fixed effect, and phylogeny and species identity as random effects. Phylogenetic heritability, a measure of phylogenetic correlation equivalent to Pagel's (1999) λ (Hadfield and Nakagawa, 2010), was estimated as the proportion of variance attributable to the random effect of phylogeny. The significance of fixed effects was tested using Wald-type *F*-tests with conditional sums of squares and denominator degrees of freedom calculated according to Kenward and Roger (1997). The significance of phylogenetic heritability was assessed using likelihood ratio tests to compare models with and without the random effect of phylogeny. Approximate standard errors for the estimate of phylogenetic heritability were calculated using

the R 'pin' function (http://www.homepages.ed.ac.uk/iwhite//asreml/).

RESULTS AND DISCUSSION
The increase in whole-animal NCOT with non-negative gradient was greater for large animals than for small ones (Table 1, Fig. 2A,B). Similarly, the increase in $NCOT_{rel}$ with gradient was also greater for large animals than for small ones (Table 1, Fig. 2B,C). However, the increase in $NCOT_{ms}$ with gradient was not affected by body mass (Table 1, Fig. 2E,F). Removing the outliers indicated in Fig. 2B, D and F does not alter this conclusion: the scaling exponent for the increase in $NCOT_{ms}$ with gradient changes very little from -0.038 ± 0.045 (mean±s.e.m.) (Table 1) to -0.046 ± 0.027 and remains non-significant. Similarly, weighting by the square root of the number of gradients for which each relationship was determined does not alter this conclusion. Phylogenetic heritability was moderate for all of these relationships, but never significantly greater than zero (Table 1).

In both absolute and relative terms, across the range of body masses analysed, lighter birds and mammals experience a smaller increase in transport energy costs when walking uphill (Fig. 2A–D). This might be interpreted as indicating that the lower mass of smaller animals provides an energy advantage on an incline. However, on a mass-specific basis, the increase in NCOT as incline angle increases is similar across birds and mammals of different size (Fig. 2E,F). These differences in the effect of incline gradient and NCOT across whole-animal, relative and mass-specific data highlight that different and apparently contradictory interpretations are possible with a single data set.

Considering all of these relationships together provides the fullest insight. On a per unit mass basis, smaller birds and mammals are not more efficient at traversing inclines; there is in fact no systematic variation across body size in the relationship between $NCOT_{ms}$ and gradient (Fig. 2F). This suggests that broadly across species, the main reason for the additional cost associated with incline

Table 1. Parameter estimates for the effect of body mass on the slope of the relationship between net cost of transport (NCOT) and gradient

Term	Estimate	s.e.m.	F (d.f.)	P
(A) Fixed=log(slope of whole-animal NCOT on gradient) ~log(M)				
Intercept	−0.319	0.067	22.6 (1,20.1)	0.0001
log(M)	0.946	0.045	444.6 (1,18.5)	<0.0001
Phylogeny	*1.00×10^{-7}*	*4.84×10^{-8}*		
Species	*0.0251*	*0.0307*		
Residual	*0.06728*	*0.0303*		
(B) Fixed=log(slope of NCOT$_{rel}$ on gradient) ~log(M)				
Intercept	−1.26	0.08	284.7 (1,19.1)	<0.0001
log(M)	0.222	0.052	18.4 (1,19.0)	0.0004
Phylogeny	*2.67×10^{-8}*	*1.96×10^{-8}*		
Species	*0.0713*	*0.0329*		
Residual	*0.0221*	*0.0162*		
(C) Fixed=log(slope of NCOT$_{ms}$ on gradient) ~log(M)				
Intercept	−1.64	0.07	579.4 (1,21.2)	<0.0001
log(M)	−0.038	0.045	0.699 (1,19.7)	0.41
Phylogeny	*1.18×10^{-8}*	*5.40×10^{-9}*		
Species	*0.0216*	*0.0298*		
Residual	*0.162*	*0.053*		

Body mass (*M*) was measured in kg and gradient in deg. (A) Whole-animal NCOT (A; J m^{-1}); (B) relative NCOT (NCOT$_{rel}$) at an incline of 0 deg; (C) mass-specific NCOT (NCOT$_{ms}$; J kg^{-1} m^{-1}).
Values in italics are estimates of the residual variance and variance associated with the random effects of phylogeny and species. Phylogenetic heritability is 0.29 ± 0.33 (mean±s.e.m.) for whole-animal NCOT ($\chi_1^2 = 0.00$, $P = 0.998$), 0.76 ± 0.19 for NCOT$_{rel}$ ($\chi_1^2 = 0.00$, $P = 1$) and 0.15 ± 0.23 for NCOT$_{ms}$ ($\chi_1^2 = 0.00$, $P = 0.999$).
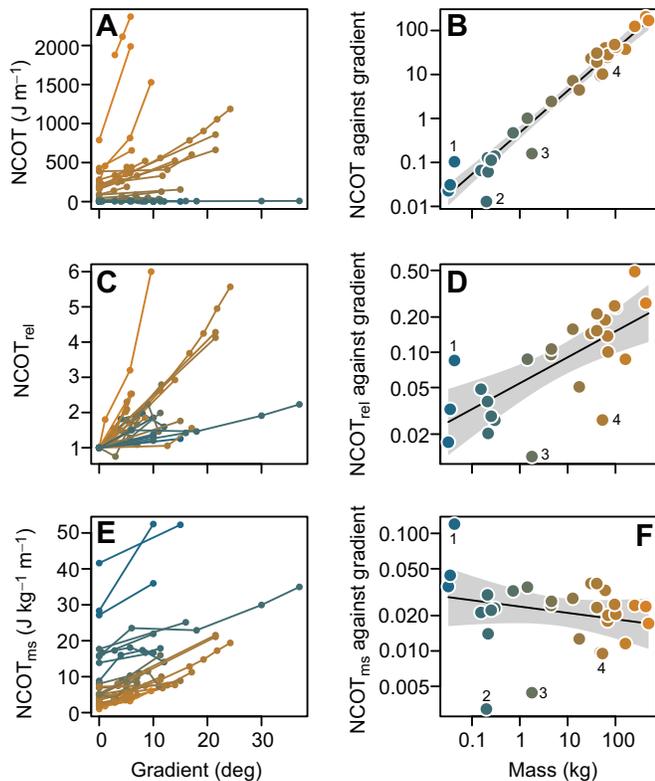
Fig. 2. Relationship between NCOT and gradient, on a per species basis. The left panels present absolute NCOT (A; $N=26$), relative NCOT ($NCOT_{rel}$, C; $N=26$) and mass-specific NCOT ($NCOT_{ms}$, E; $N=23$) plotted against gradient. Lines link data for the same species. The right panels show the slopes of the linear regressions of NCOT against gradient (B), $NCOT_{rel}$ against gradient (D) and $NCOT_{ms}$ against gradient (F), all plotted against body mass. The data are coloured by $\log_{10}$(mass) from lightest species (blue) to heaviest (orange). Solid lines in panels B, D and F show the relationships between $\log_{10}$(NCOT), $\log_{10}(NCOT_{rel})$ and $\log_{10}(NCOT_{ms})$ and body mass, respectively, calculated using the phylogenetically informed parameter estimates in Table 1. Grey areas enclose the 95% confidence interval of the regression. Species identified in B, D and F are those with relatively extreme values: 1, king quail *Coturnix chinensis* weighing 0.043 kg; 2, brown rats *Rattus norvegicus* weighing 0.2 kg; 3, barnacle geese *Branta leucopsis* weighing 1.79 kg; and 4, lions *Panthera leo* weighing 53.5 kg. Raw data and sources are provided in Table S1.

locomotion is an extrinsic one – the cost to raise the body's mass against gravity (Borghols et al., 1978; Full and Tullis, 1990; Lees et al., 2013) – as this should drive an increase in metabolic costs that is proportional to body mass if the metabolic efficiency of vertical locomotion is independent of mass. However, the energy cost for small animals to run on the flat per unit mass is greater than that for larger animals (Full and Tu, 1991; Pontzer, 2016) – smaller animals are intrinsically less efficient movers – and thus the additional cost that smaller animals incur when running on an incline due to working against gravity is relatively small (Fig. 2C,D).

Ecological perspectives

The concept of energy landscapes (Wilson et al., 2011) allows analyses of animal transport costs to be placed within an ecological context (Halsey, 2016). Quantification of energy landscapes will provide insight into the movement pathways taken by animals. It is likely that in many cases slope angle is the most important driver of variation in transport costs and thus, in turn, movement pathways (Shepard et al., 2013). For example, an animal seeking

to minimise its energy outlay, perhaps because energy availability in the environment is low and thus it is striving to use its energy stores judiciously, or because it has limited ability to dissipate metabolically produced heat (Speakman and Krol, 2010), is expected to move in predictable ways within its landscape, repeatedly using low-cost routes (Rees, 2004). Because absolute and relative NCOT are greater for heavier animals moving up inclines (Fig. 2B,D), we might reasonably expect bigger animals to be more inhibited in the routes they take across their energy landscape.

Where judicious use of energy stores is the focus, an animal may be less prohibited to climb across a mountainous landscape if the additional costs of moving uphill are offset by a concomitantly reduced NCOT when moving down the same incline. In such a scenario the 'broad scale' energy landscape therefore flattens. Hypothetically, smaller animals may expend less energy braking to limit their speed when going downhill because they are more stable, less at risk of injury and/or their mass is a small component in determining force compared with gravitational acceleration (Birn-Jeffery and Higham, 2014). In turn, smaller animals may experience a considerable 'reimbursement' of the additional energy expended going uphill when they then travel downhill. In contrast, larger animals may tend to expend considerable additional energy on a decline to control their velocity. The data for NCOT on declines is presently rather limited; however, according to the bird and mammal data available, it seems likely that at least for those species represented, the additional energy expended when moving up an incline is not offset by reduced NCOT when moving down the same incline. This is because the relationship between NCOT and gradient is probably non-linear for negative inclines, in that the positive slope of the relationship between NCOT and incline gradient is reduced or even reversed for decline gradients (Fig. 1). Additional detailed measurements of NCOT, particularly for smaller species, at a range of positive and negative inclines are necessary to explore these concepts further.

The documented routes of African elephant herds support the proposition that bigger animals tend to be more inhibited in the routes they take across their energy landscape. The movements of many groups of elephants observed in southern Africa are apparently constrained by the topography of their home ranges in that they rarely walk on ground where the incline is more than about 4 deg (Roever et al., 2012). Wall et al. (2006) argue that this selective behaviour against walking uphill is due to the massive energy costs of doing so for an animal typically weighing several tonnes. They reported on a herd, which foraged everywhere in their territory except on the single prominent hill, despite the presence of lush vegetation at its peak, and estimated that the cost to climb the hill for an adult elephant would be around 10,000 kJ. Famously, in 218 BC, Hannibal lost many of his war elephants to emaciation while crossing the Alps.

Our analyses show that because of their large size, elephants will experience not just an absolute but a relatively high increase in NCOT when incline walking. The elephants studied by Wall et al. (2006) already forage for 16–18 h per day, so perhaps they could not easily compensate for the additional food intake required to fuel their locomotion uphill. Similarly, it is possible that the resultant additional heat generated by incline locomotion at a worthwhile speed could not be readily dissipated from their bodies (Speakman and Krol, 2010). However, there are also other possible explanations for the herd's reluctance to walk uphill, based on fundamental scaling principles. For geometrically similar animals, body mass scales with the cube of linear dimensions of body size while muscle

cross-sectional area scales with the square, such that the relative power an animal can generate decreases with size (Schmidt-Nielsen, 1984); larger animals might therefore be limited in the slope inclines they can ascend by the power they can generate to walk at a worthwhile speed. Bone cross-sectional area also scales with the square of body size and thus larger animals may also be less inclined to walk on slopes because of their relatively high risk of injury if they fall.

Large animals that move around the landscape with little regard for slope angle may highlight the importance of other factors in shaping their movement patterns (Shepard et al., 2013). For example, re-analysis of the data presented by Reichman and Aitchison (1981) reveals little evidence that the inclines of the paths chosen by mountain-dwelling mammals in the snow relate to their body mass; both small and large animals readily took paths with both small and large inclines. In this respect, power output appears not to have been limiting to the larger species, and perhaps the time the animals spent walking on inclines was sufficiently small that the energy costs to do so were outweighed by advantages such as time savings and predator avoidance.

Conclusions

For their size, lighter birds and mammals expend a lot of energy to move uphill. This is mainly because their unit-mass cost to run on the flat is high; they are intrinsically uneconomical runners. Because they have low absolute locomotion costs, the additional cost associated with movement across hilly ground is small. The energy costs to move uphill are also low in relative terms for small animals and thus inclined ground is unlikely to have a strong influence on their choice of route through an environment; the energy landscape presented to them is relatively flat even when the physical landscape is sloping upwards. Our study demonstrates the value and importance of considering costs of animal locomotion in absolute, relative and mass-specific terms. This would ensure a clearer understanding of the relationships between cost of transport and body mass, providing both mechanistic insights to the relationships and an understanding of their ecological implications. We argue that our findings also act as a case study demonstrating the general value of interrogating measures of metabolic rate in different forms to support data interpretation.

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