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

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Running head: Transport costs to run uphill

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16 **Abstract**

17 Comparative work on animals' costs of terrestrial locomotion has focussed on the underpinning

18 physiology and biomechanics. Often, much of an animal's energy budget is spent on moving around

19 thus there is also value in interpreting such data from an ecological perspective. When animals move

20 through their environment they encounter topographical variation, and this is a key factor that can

21 dramatically affect their energy expenditure. We collated published data on the costs for birds and

22 mammals to locomote terrestrially on inclines, and investigated the scaling relationships using a

23 phylogenetically informed approach. We show that smaller animals have a greater mass-specific cost

24 of transport on inclines across the body mass range analysed. We also demonstrate that the increase

25 in cost for smaller animals to run up a slope relative to along a flat surface is comparatively low.

26 Heavier animals show larger absolute and relative increases in energy cost to travel uphill.

27 Consideration of all aspects of the cost of incline locomotion – absolute, relative, and mass-specific –

28 provides a fuller understanding of the interactions between transport costs, body mass, incline

29 gradient and phylogeny, and enables us to consider their ecological implications, which we couch

30 within the context of the 'energy landscape'.

31

32 **Introduction**

33 Comparative analyses of the energy expended by animals to locomote have shed light on how their

34 size relates to the costs for them to move around their environment. While in absolute terms the

35 metabolic cost of terrestrial locomotion increases with an animal's size, per unit mass this cost is

36 lower in larger species (Full et al., 1990; Schmidt-Nielsen, 1972; Taylor et al., 1970). However, most

37 of these data have been derived from animals running on the flat while natural environments often

38 encompass sloping ground, which is another factor likely to have a large effect on animals' energy

39 transportation costs. Thus a better understanding of the energy expended by wild animals when

40 traversing a landscape is gained from measurements of movement costs on different gradients.

41 Recently, several papers have analysed across-species relationships between the net cost of

42 transport (NCOT; ml O_2 m^{-1}), the incline of the ground being walked on and animal body mass.

43 Snyder and Carello (2008) provide evidence that the efficiency of animals in converting metabolic

44 energy into vertical work when walking up a slope increases with body mass up to around 1 kg, and

45 both Tullis and Andrus (2011) and Lees et al. (2013) indicate that per unit mass the cost for an

46 animal to move uphill is lower for larger species, again up to a mass of about 1 kg. The interpretation

47 from all of these studies is that the energy disadvantage experienced by particularly small terrestrial

48 animals when walking on the flat is exacerbated on an incline.

49 However, these previous analyses all considered inter-specific scaling of the cost of transport on a

50 mass-specific basis. Such 'pound for pound' analyses facilitate comparisons between species of

51 greatly varying sizes, and provide a means for determining the mechanisms underlying inter-specific

52 correlations. However, since mass-specific values do not reflect the absolute energy expenditure for

53 an animal they may also not reflect the ecological consequences to the animal of those metabolic

54 costs.

55 Furthermore, concern has been raised (Lees et al., 2013) that inherent confounds limit the

56 comparative power of the incline NCOT data available in the literature (Lees et al., 2013; Tullis and

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

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

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

81 **Materials and Methods**

82 Data for NCOT (ml O_2 m^{-1}) were compiled from the peer-reviewed literature, from studies where
83 animals were run at more than one gradient, and were converted to J m^{-1} assuming an energy
84 equivalence of O_2 of 20.1 J ml^{-1}. NCOT was defined as the slope of a linear regression relating
85 metabolic rate and speed of terrestrial locomotion at a fixed incline. In all studies included, the
86 animals always ran directly along the treadmill in a cranial-caudal direction. The speeds and slopes
87 applied were selected by the experimenters. Where NCOT values were not supplied, data were
88 digitized for regression analysis. In total, data were collected and analysed for 24 species, ranging in
89 mass from the 30 g mouse *Mus musculus* to the 492 kg horse *Equus ferus*. Mass values for each
90 species were compiled from the same studies from which NCOT data were compiled. Although data
91 were available in the literature for many groups of animals locomoting on inclines up to 90°, we
92 limited the analysis to birds and mammals on inclines less than 90° to ensure that there was no
93 association between body mass and incline in the data set (the largest incline in the data set was
94 37°, and we excluded one measurement of NCOT for humans climbing up a vertical wall (Booth et
95 al., 1999). For each data set, we calculated the slope of the relationship between NCOT (J m^{-1}) or
96 mass-specific NCOT (J kg^{-1} m^{-1}) and gradient (°) using linear regression. For data sets where animals
97 were measured running on the level (0°; all but three data sets), we also calculated relative NCOT by
98 dividing all NCOT values by the value of NCOT measured at 0°, and then calculated the slope of the

99   line relating relative NCOT to gradient. For some species, data were available from more than one
100   study, or for more than one cohort of animals. In these cases, each study or cohort was analysed as a
101   separate data set, except for the study of Lees et al. (2013), for which winter and summer animals
102   were pooled (NCOT increased with incline for both winter and summer birds in this study, but the
103   magnitude of the increase was inconsistent with other studies unless the data were pooled). Studies
104   of elk (Cohen et al., 1978), reindeer (Fancy and White, 1987), and mountain goats and bighorn sheep
105   (Dailey and Hobbs, 1989) all provided unique mean mass values for each gradient, and so these were
106   averaged for analysis.

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

120   Data were analysed using phylogenetic mixed models (Hadfield and Nakagawa, 2010; Housworth et
121   al., 2004; Lynch, 1991) implemented in the ASReml-R (Gilmour et al., 2009) package of R v3.0.2 (R
122   Core Team, 2013). Phylogenetic mixed models were selected over the more commonly used
123   methods of independent contrasts (Felsenstein, 1985; Rezende and Diniz-Filho, 2012) and
124   phylogenetic generalised least squares (Grafen, 1989; Rezende and Diniz-Filho, 2012) because
125   phylogenetic mixed models can formally incorporate phylogenetic non-independence as well as non-
126   independence associated with multiple measurements of single species (i.e. multiple studies of the
127   same species). The tree used for analysis was constructed using published trees for mammals
128   (Bininda-Emonds et al., 2007) and birds (Jetz et al., 2012). The mammal tree was constructed using a
129   formal supertree approach to combine published trees estimated by a range of methods (Bininda-
130   Emonds, 2004), and was built using an explicit source tree collection protocol that minimized data
131   duplication and the inclusion of source trees of lesser quality, such as those based on taxonomy. The
132   bird tree was assembled using a sequence data for four protein coding mitochrondrial genes
133   (cytochrome b, 4902 species; cytochrome oxidase I, 2335 species; NADH dehydrogenase subunit 2,
134   4308 species; and NADH dehydrogenase subunit 3, 1232 species), and six nuclear loci
135   (recombination activating protein 1 [rag-1], 1528 species; beta-fibrinogen intron 5 [bfib5] 5, 1089
136   species; beta-fibrinogen intron 7 [bfib7], 1460 species; glyceraldehyde 3-phosphate dehydrogenase
137   [gapdh], 967 species; myoglobin [myo], 1867 species; and ornithine decarboxylase [odc], 1405
138   species), which was combined with taxonomic information for species lacking sequence data to build
139   trees for each of 158 clades that were then grafted onto a backbone phylogeny (Hackett et al.,
140   2008). For birds, we constructed a single majority rule consensus tree from the published posterior
141   distribution of 10,000 trees (Jetz et al., 2012) using 'ape' v3.1-1 (Paradis et al., 2004). For the
142   combined mammal and bird tree, branch lengths estimated using Grafen's (1989) arbitrary branch

143 length transformation (branch lengths set to a length equal to the number of descendant tips minus
144 one).

145 The models included $\log_{10}$-transformed data for the slope of NCOT on gradient, the slope of mass-
146 specific NCOT on gradient, or the slope of relative NCOT on gradient as the dependent variable,
147 $\log_{10}$(body mass, kg) as a fixed effect, and phylogeny and species identity as random effects.
148 Phylogenetic heritability, a measure of phylogenetic correlation equivalent to Pagel's (1999) λ
149 (Hadfield and Nakagawa, 2010), was estimated as the proportion of variance attributable to the
150 random effect of phylogeny. The significance of fixed effects was tested using Wald-type F-tests with
151 conditional sums of squares and denominator degrees of freedom calculated according to (Kenward
152 and Roger, 1997). The significance of phylogenetic heritability was assessed using likelihood ratio
153 tests to compare models with and without the random effect of phylogeny. Approximate standard
154 errors for the estimate of phylogenetic heritability were calculated using the R 'pin' function (White,
155 2013).

Results

157 The increase in whole-animal NCOT with non-negative gradient was greater for large animals than
158 small ones (Table 1, Figure 2A,B). Similarly, the increase in relative NCOT with gradient was also
159 greater for large animals than for small ones (Table 1, Figure 2B,C). However, the increase in mass-
160 specific NCOT with gradient was not affected by body mass (Table 1, Figure 2E,F). Removing the
161 outliers indicated in Figures 2B, 2D, and 2F does not alter this conclusion: the scaling exponent for
162 the increase in mass-specific NCOT with gradient changes very little from -0.038 ± 0.045 [SE] (Table
163 1) to -0.046 ± 0.027 and remains non-significant. Similarly, weighting by the square root of the
164 number of gradients for which each relationship was determined does not alter this conclusion.
165 Phylogenetic heritability was moderate for all of these relationships, but never significantly greater
166 than zero (Table 1).

Discussion

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

175 Considering all of these relationships together provides the fullest insights. On a per unit mass basis,
176 smaller birds and mammals are not more efficient at traversing inclines; there is in fact no
177 systematic variation across body sizes in the relationship between mass-specific NCOT and gradient
178 (Figure 2F). This suggests that broadly across species, the main reason for the additional cost
179 associated with incline locomotion is an extrinsic one - the cost to raise the body's mass against
180 gravity (Borghols et al., 1978; Full and Tullis, 1990; Lees et al., 2013), since this should drive an
181 increase in metabolic costs that is proportional to body mass if the metabolic efficiency of vertical
182 locomotion is independent of mass. However, the energy costs for small animals to run on the flat
183 per unit mass are greater than for larger animals (Full and Tu, 1991; Pontzer, 2016) – smaller animals

184   are intrinsically less efficient movers - and thus the additional cost smaller animals incur when
185   running on an incline due to working against gravity is relatively small (Figure 2C,D).

186   The concept of energy landscapes (Wilson et al., 2011) allows analyses of animal transport costs to
187   be placed within an ecological context (Halsey, 2016). Quantification of energy landscapes will
188   provide insight into the movement pathways taken by animals. It is likely that in many cases slope
189   angle is the most important driver of variation in transport costs and thus, in turn, movement
190   pathways (Shepard et al., 2013). For example, an animal seeking to minimise its energy outlay,
191   perhaps because energy availability in the environment is low and thus it is striving to use its energy
192   stores judiciously, or because it has limited ability to dissipate metabolically produced heat
193   (Speakman and Krol, 2010), is expected to move in predictable ways within its landscape, repeatedly
194   using low-cost routes (Rees, 2004). Because absolute and relative NCOT is greater for heavier
195   animals moving up inclines (Figure 2B, D), we might reasonably expect bigger animals to be more
196   inhibited in the routes they take across their energy landscape.

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

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

224   Our analyses show that due to their large size, elephants will experience not just an absolute but a
225   relatively high increase in NCOT when incline walking. The elephants studied by Wall et al. (2006)

226 already forage for 16-18 hours per day, so perhaps they could not easily compensate for the
227 additional food intake required to fuel their locomotion uphill. Similarly, it is possible that the
228 resultant additional heat generated by incline locomotion at a worthwhile speed could not be readily
229 dissipated from their bodies (Speakman and Krol, 2010). However, there are also other possible
230 explanations for the herd's reluctance to walk uphill, based on fundamental scaling principles. For
231 geometrically similar animals, body mass scales with the cube of linear dimensions of body size while
232 muscle cross-sectional area scales with the square such that the relative power an animal can
233 generate decreases with size (Schmidt-Nielsen, 1984); larger animals might therefore be limited in
234 the slope inclines they can ascend by the power they can generate to walk at a worthwhile speed.
235 Bone cross-sectional area also scales with the square of body size and thus larger animals may also
236 be less inclined to walk on slopes because of their relatively high risk of injury if they fall.

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

245 *Conclusions*

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

258

262 **Competing interests**

263 The authors have no competing interests.

264

Author contributions

LGH and CRW devised the study, LGH collated the data, CRW led on the analyses and barbequing, while LGH led on the write-up.

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Table 1. Parameter estimates for the effect of body mass (M, kg) on the slope of the relationship between net cost of transport (NCOT) on gradient (°), with NCOT expressed as whole-animal NCOT (A, J m^{-1}), NCOT expressed relative to NCOT at an incline of 0° (B, relative NCOT), and mass-specific NCOT (C, J kg^{-1} m^{-1}).

A) Fixed = Log(slope of whole-animal NCOT on gradient) ~ log(M)

Term	Estimate	SE	*F* (df)	P
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 x 10^{-7}*	*4.84 x 10^{-8}*		
Species	*0.0251*	*0.0307*		
Residual	*0.06728*	*0.0303*		

B) Fixed = Log(slope of relative NCOT on gradient) ~ log(M)

Term	Estimate	SE	*F* (df)	P
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 x 10^{-8}*	*1.96 x 10^{-8}*		
Species	*0.0713*	*0.0329*		
Residual	*0.0221*	*0.0162*		

C) Fixed = Log(slope of mass-specific NCOT on gradient) ~ log(M)

Term	Estimate	SE	*F* (df)	P
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 x 10^{-8}*	*5.40 x 10^{-9}*		
Species	*0.0216*	*0.0298*		
Residual	*0.162*	*0.053*		

Parameters in italics are estimates of the residual variance and variances associated with the random effects of phylogeny and species. Phylogenetic heritability is 0.29 ± 0.33 [SE] for whole animal NCOT (χ^2_1 = 0.00, P = 0.998), 0.76 ± 0.19 for relative NCOT (χ^2_1 = 0.00, P = 1), and 0.15 ± 0.23 for mass-specific NCOT (χ^2_1 = 0.00, P = 999).
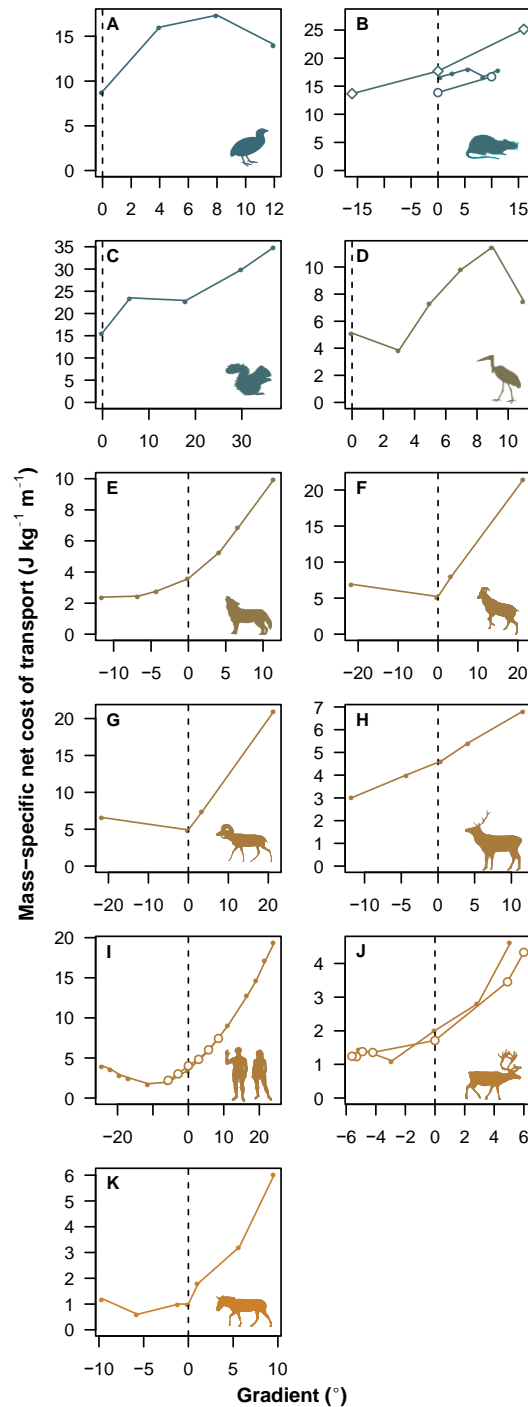
Figure 1. The relationship between mass-specific net cost of transport and gradient for species measured over more than three gradients (irrespective of whether those gradients were negative or non-negative). A: common quail *Coturnix coturnix*, B: brown rat *Rattus norvegicus* (filled circles: 0.20 kg; unfilled circles: 0.22 kg; unfilled 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; unfilled symbols: 70 kg), J: caribou *Rangifer tarandus* (filled symbols: 96 kg; unfilled symbols: 102 kg), K: horse *Equus ferus asinus*. Data and sources are provided in the supplementary material. Original image for pine squirrel © John Plaistow and licenced 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).
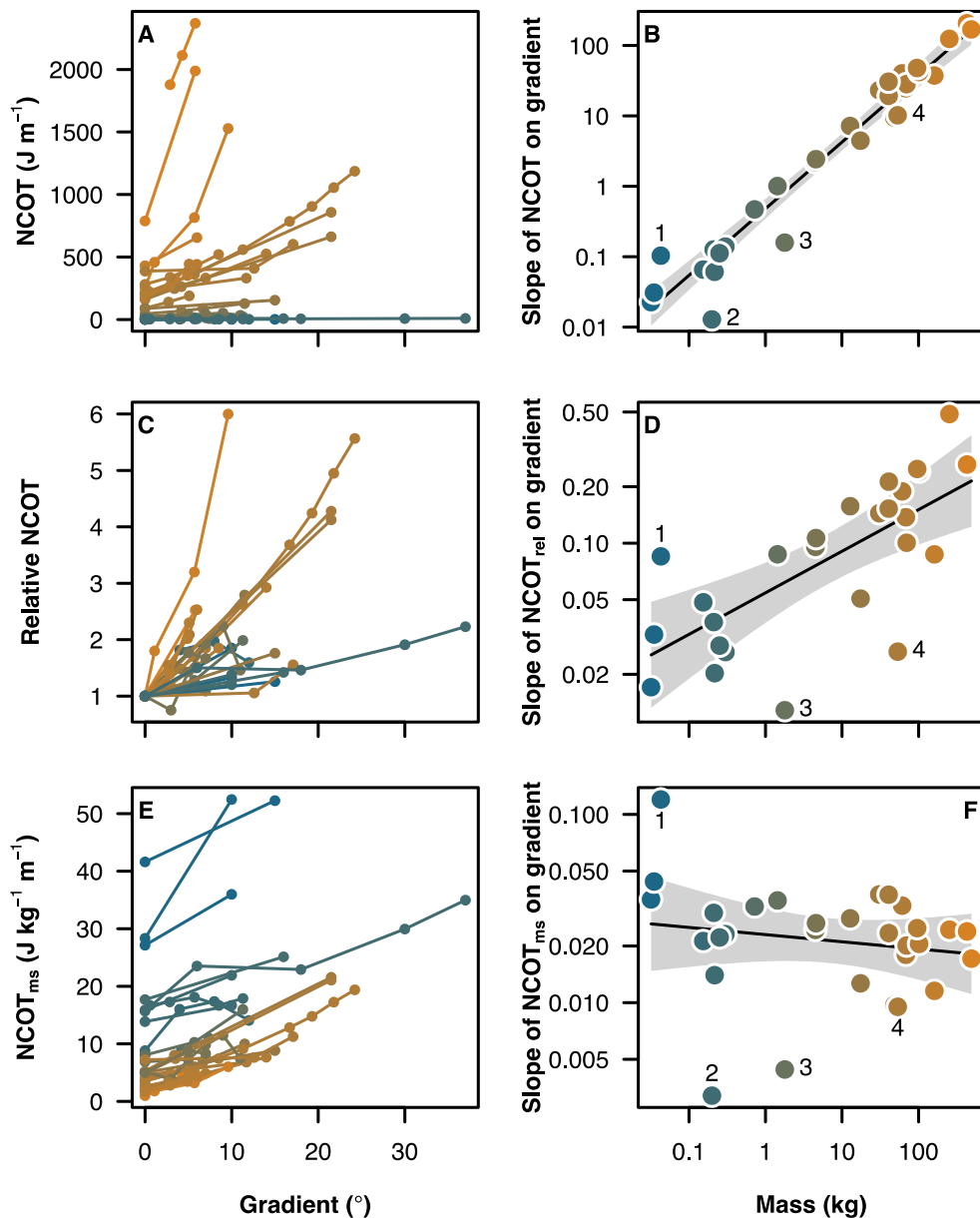
Figure 2. Relationships between NCOT and gradient, on a per species basis. The left panels present NCOT as absolute (A, J m^{-1}; n = 26), relative (C, n = 26), and mass-specific (E, J kg^{-1} m^{-1}; n = 23). Lines link data for the same species. The right panels shows the slopes of the linear regressions of NCOT against gradient (B), relative NCOT against gradient (NCOT$_{rel}$, D), and mass-specific NCOT against gradient (NCOT$_{ms}$, F), all plotted against body mass (kg). 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$_{ms}$), respectively, calculated using the phylogenetically informed parameter estimates in Table 1. Grey areas enclose the 95% confidence interval of the regression. Species identified in panels 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 the supplementary material.

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