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Research

Path tortuosity changes the transport cost paradigm in terrestrial animals

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The time that animals spend travelling at various speeds and the tortuosity of their movement paths are two of the many things that affect space-use by animals. In this, high turn rates are predicted to be energetically costly, especially at high travel speeds, which implies that animals should modulate their speed according to path characteristics. When animals move so as to maximize distance and minimize metabolic energy expenditure, they travel most efficiently at the speed that gives them a minimum cost of transport (COT_{min}), a well-defined point for animals that move entirely in fluid media. Theoretical considerations show though, that land animals should travel at their maximum speed to minimize COT, which they do not, instead travelling at walking pace. So, to what extent does COT_{min} depend on speed and turn rate and how might this relate to movement paths? We measured oxygen consumption in humans walking along paths with varied tortuosity at defined speeds to demonstrate that the energetic costs of negotiating these paths increase disproportionately with both speed and angular velocity. This resulted in the COT_{min} occurring at very low speeds, and these COT_{min} speeds reduced with increased path tortuosity and angular velocity. Logged movement data from six free-ranging terrestrial species underpinned this because all individuals turned with greater angular velocity the slower their travel speeds across their full speed range. It seems, therefore, that land animals may strive to achieve minimum movement costs by reducing speed with increasing path variability, providing one of many possible explanations as to why speed is much lower than currently predicted based on lab measurements of mammalian locomotor performance.

Keywords: angular velocity, energy landscape, minimum cost of transport, movement paths, preferred walking speed, track tortuosity

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Introduction

Movement is a fundamental tenet of the animal kingdom, with animals moving at varying speeds in chosen directions to use space over time in defined ways that is presumed to enhance their survival and lifetime reproductive success (Williams et al. 2002). Movement requires energy, which varies according to the speed of the animal (Dickinson et al. 2000). The speed that an animal selects for movement, and therefore the energy designated to it over time, depends on the purpose of the movement because locomotor efficiency may be less important than the behavioural role of locomotion (Wilson et al. 2015) which may depend on a variety of currencies including time or reproductive success (Shepard et al. 2009). There are three primary reasons for this: 1) animals may move at any speed, including their maximum, to evade predators or capture prey (Williams et al. 2014), to maximize net rate of acquisition of food energy (Wilson et al. 2002) or to provide young with food at an appropriate rate for their growth (Shepard et al. 2009); 2) animals may move at a speed that minimizes power costs (a concept that is primarily applicable for flying animals) (Tucker 1973). In addition, 3) animals may move at a speed that minimizes the cost of transport (COT_{min} speed), maximizing the distance travelled per unit of energy (Tucker 1970, Watanabe et al. 2011). This last paradigm (Taylor et al. 1970) is particularly important because most travel is assumed to be under strong selection pressure for animals to maximize output while minimizing input, which occurs at COT_{min} (Langman et al. 2012, van der Hoop et al. 2014). The COT_{min} speed is well defined for any instance where power for movement increases with speed at a greater than linear rate, such as in aquatic and volant animals. Indeed, wild animals moving entirely in fluid media generally travel at these speeds (Pennycuick et al. 2013) although there are exceptions, for instance when birds are minimizing power alone or when saving time is a more important currency than saving energy (Hedenström and Alerstam 1996). However, most terrestrial animals have a linear relationship between power and speed (Taylor et al. 1970, 1982) and therefore, because COT is derived by dividing the power by the speed, COT in these animals will always decrease with increasing speed. In short, the lowest theoretical costs of transport in terrestrial animals should occur at their maximum speeds (but see Hoyt and Taylor 1981, Daley et al. 2016). Yet these are not the speeds at which animals normally travel as they move through their environment in natural contexts (Schooley et al. 1996). Although the probability of accident and injury increases at very high speeds (Wynn et al. 2015), which is a clear reason to avoid them unless there is a compelling motive to sprint (e.g. in cursorial predators and their prey (Wilson et al. 2018)), there is currently no energy-based explanation as to why land animals travel through their environments at their normal chosen speeds.

Based on recent studies that found that the costs associated with turning are substantial (Wilson et al. 2013, McNarry et al. 2017), we hypothesized that track tortuosity should therefore alter the speed of COT_{min} in terrestrial animals. To test this, we set up experiments to gain empirical data on how speed and angular velocity in humans relate to energy expenditure and thereby to the cost of transport. At the same time, we equipped six species of free-living animal with tags that allowed us to study animal speed in tandem with angular velocity to see how our physiological findings translated into patterns of movement in the natural environment.

Material and methods

Participants

Twenty able-bodied male participants (mean ± SD: age 30 ± 8 years; body mass 75.6 ± 11.2 kg; stature 1.78 ± 0.06 m; body mass index: 24.0 ± 3.2 $kg·m^{-2}$) gave their written informed consent to volunteer for this study. Stature (Holtain, Crymych, UK) was measured to the nearest 0.01 m and body mass (Seca, Germany) to the nearest 0.01 kg.

Trials

Participants walked at four different speeds (0.69, 0.97, 1.25 and 1.53 $m\ s^{-1}$) and four turn angle extents (0, 90, 135 and 180°), giving a total of sixteen speed and angle combinations. Separate walking tracks were marked onto a flat-surfaced sports lab floor using tape for each angle of interest. Each track alternated between 5 m straight lines and turns with equal numbers of left and right turns (0°: a 25 m straight line with markers every 5 m; 90°: two squares sharing one 5 m straight; 135°: two eight-angled star polygons sharing a 5 m straight; 180°: a 5 m straight). Participants' average walking speed was controlled using a metronome at either 8, 12, 15 or 18 bpm. Participants walked barefooted, carried out only step-turns (not spin-turns), and reached a corner (or 5 m mark) on each metronome beat (i.e. travelled 5 m between beats). Walking conditions were block-randomized by turning angle: all speed trials for a given angle were conducted before moving on to the next angle, but average travel speed and the sequence in which the angle conditions were completed by each participant were randomized and counterbalanced. Each walking condition lasted 3 min to allow achievement of a metabolic steady state, and each condition was separated with 3-min of quiet seated rest.

Respirometry

A portable and wireless breath-by-breath respirometry system (MetaMax 3B-R2, Cortex, Biophysik, Leipzig, Germany) was used to measure rates of oxygen consumption (VO_2, $l\ min^{-1}\ kg^{-1}$, see the Supporting information for an example trace) and carbon dioxide production (VCO_2, $l\ min^{-1}\ kg^{-1}$). The system (1.4 kg) was attached to each participant using a harness with the weight of battery and sensors (infrared analyser and electrochemical cell for CO_2 and O_2 measurements, respectively) equally divided between the left and right sides of the chest. Volume of inspired/expired gas was measured using a bidirectional digital turbine fitted within a mask (Hans Rudolph 7450 Series V2) from which a sample of gas was extracted via a 60 cm sampling tube for gas analysis. Prior to each trial, reference gases were used to calibrate the O_2 and CO_2 analysers and the turbine volume transducer was calibrated using a 3 l syringe (Hans Rudolph, Kansas City, MO). VO_2 and VCO_2 were calculated using continuous measurements of F_IO_2 and F_ICO_2 and the Haldane transformation. Metasoft 3 software ver. 3.7.0 SR2 was used to monitor traces during trials and export data. Respiratory exchange ratios (VCO_2:VO_2) and their thermal equivalents taken from (Brody 1945) were used to convert VO_2 to metabolic power (P_{met}, W kg^{-1}). The cost of transport (J kg^{-1} m^{-1}) was calculated by dividing P_{met} by average travel speed (m s^{-1}).

Identifying angular velocity from turns

All participants were equipped with a lower back, mid-line mounted 'Daily Diary' tag (Wilson et al. 2008) recording tri-axial (orthogonal) acceleration and magnetic field intensity at 40 Hz. Post-experiment, all magnetic field data were plotted on a tri-axial spherical plot of magnetic field intensity (m-sphere; see Williams et al. 2017 for details). While participants walking in straight-lines led to little variation in tri-axial plotted position on the m-sphere, those that executed turns resulted in rapid movement of points across the m-sphere surface which clearly showed at which points turns began and ended so that turn duration could be derived. Maximum resolution for this was 1/40th second. The duration of turns was determined for five turns per individual per speed and turn angle combination.

Derivation of costs

Metabolic measurements for the 0° trials were corrected for the costs of 180° turns that were necessary at the end of every 25 m of straight-line walking. In order to calculate the cost of transport for straight line walking, a series of calculations were undertaken. Firstly, the time taken, t, to travel one length (either 5 m or 25 m) and execute one turn for any given track was calculated as distance travelled divided by speed, d/v. The total mass-specific cost of walking one length and executing one turn was then calculated as the time taken × P_{met} (tP_{met}). The total mass-specific cost of walking in a straight line for 20 m was then calculated by subtracting the mass-specific cost of walking 5 m + 1 turn in 180° trials from 25 m + 1 turn in the 0° trials; $T_{CoW} = tP_{met}|_{d=25} - tP_{met}|_{d=5}$. The total mass-specific cost of walking in a straight line for 20 m was then divided by 20 in order to derive the total mass-specific cost of transport (J kg^{-1} m^{-1}). Turn costs for any given speed and angle combination were calculated by subtracting 5 × the cost of transport for straight-line walking from the total mass-specific cost of walking 5 m and executing one turn. Each participant's turn costs were divided by their mean turn durations in order to calculate turn power (W kg^{-1}). Costs of transport were determined by dividing power by speed and the minima for the various speeds were derived from the best fit curves.

Animal tagging

Five wild mammal species (African lions *Pathera leo*, chamois *Rupicapra rupicapra*, ibex *Capra ibex*, mouflon *Ovis orientalis* and wild boar *Sus scrofa*) and one domestic mammal (domestic goat *Capra aegagrus*), which was allowed to range freely, were fitted with collar-mounted GPS-enabled 'Daily Diary' tags (Wilson et al. 2008) recording tri-axial magnetic field intensity and tri-axial acceleration at 10–40 Hz (see species-specific details in Table 1). Tags were left in place for between 15 and > 250 days before being retrieved. Downloaded data were treated to determine movement patterns using dead-reckoning as described in Bidder et al. (2015), correcting for drift using the periodic GPS positions (Bidder et al. 2015). From these data, a random period (24–50 h) was isolated from each individual, with some variation in durations to ensure that appreciable movement had taken place. For these periods, the vectorial dynamic body acceleration (VeDBA), a good proxy for speed (Bidder et al. 2012a, b), was calculated according to Qasem et al. (2012) as well as the angular velocity over one second at approximately 10 s intervals so as to give ca 20 000 angular velocity-VeDBA pairs per individual. Data from five individuals for all species were used in this manner except for the mouflon, where only four animals were used.

Statistical analyses

Linear mixed-effects models (lme4 package (ver. 1.1-26) in R Studio ver. 4.0.3) were conducted in order to investigate the relationship between angular velocity and average travel speed with differing angle extent; angular velocity with angle

Table 1. Details of tag deployments on free living animals.

Species	No.	Study area	Body mass (kg)	Tag weight (g)	Tag weight as % body weight	Deployment period	Deployment length (days)
Panthera leo	5	Kalahari, S. Africa	62–66.5	1240–1330	< 2	February 2019	18–21
Rupicapra rupicapra	5	Les Bauges, France	39.82	450	1.13	June 2017–May 2018	> 250
Capra ibex	5	Belledonne, France	28.8	450	0.64	April 2017–March 2018	> 250
Ovis gmelini	4	Caroux-Espinouse, France	50	450	0.90	May 2017–April 2018	> 250
Sus scrofa	5	Kostelec, Czech republic	6.15–10.63	850	0.8–1.3	May–Oct 2019	30–120
Capra aegagrus	5	Les Bauges, France	39.84	510	1.28	August–September 2017	29

extent at different speeds, mass-specific metabolic parameters and speed with different angle extent; and mass-specific metabolic parameters with angular velocity at different speeds or angle extent. Participant identity was included in the models as a random factor. The F statistic and marginal and conditional R^2 were determined using the car (ver. 3.0-5) and ‘MuMIn (ver. 1.43.6) packages, respectively.

Results

Empirical data from humans show how increasing track tortuosity reduces the minimum cost of transport speed to a slow walk

Our calculations of power-use by participants walking variously angled courses showed a significant interaction effect between walking speed and turn angle on total mass-specific metabolic power ($\text{speed}^2 \times$ angle category, $F = 101.81$, $p < 0.001$), with the rate of increase in power for a given increase in travel speed increasing disproportionately with turn angle (Fig. 1a, Table 2). Accordingly, there was a significant interaction effect between walking speed and turn angle on the total mass-specific cost of transport ($\text{speed}^2 \times$ angle category, $F = 59.13$, $p < 0.001$) (Fig. 1b, Table 2). The cost of transport curve showed distinct minima for paths incorporating turns, becoming more U-shaped, and with COT_{min} shifting to progressively lower walking speeds with increasing turn angle (Fig. 1b).

3-D plots of the interrelationship between metabolic power or the cost of transport with speed and angular velocity demonstrate how power increased disproportionately with increasing angular velocity, which resulted in clear COT_{min} that did not occur at the higher walking speeds. Rather,

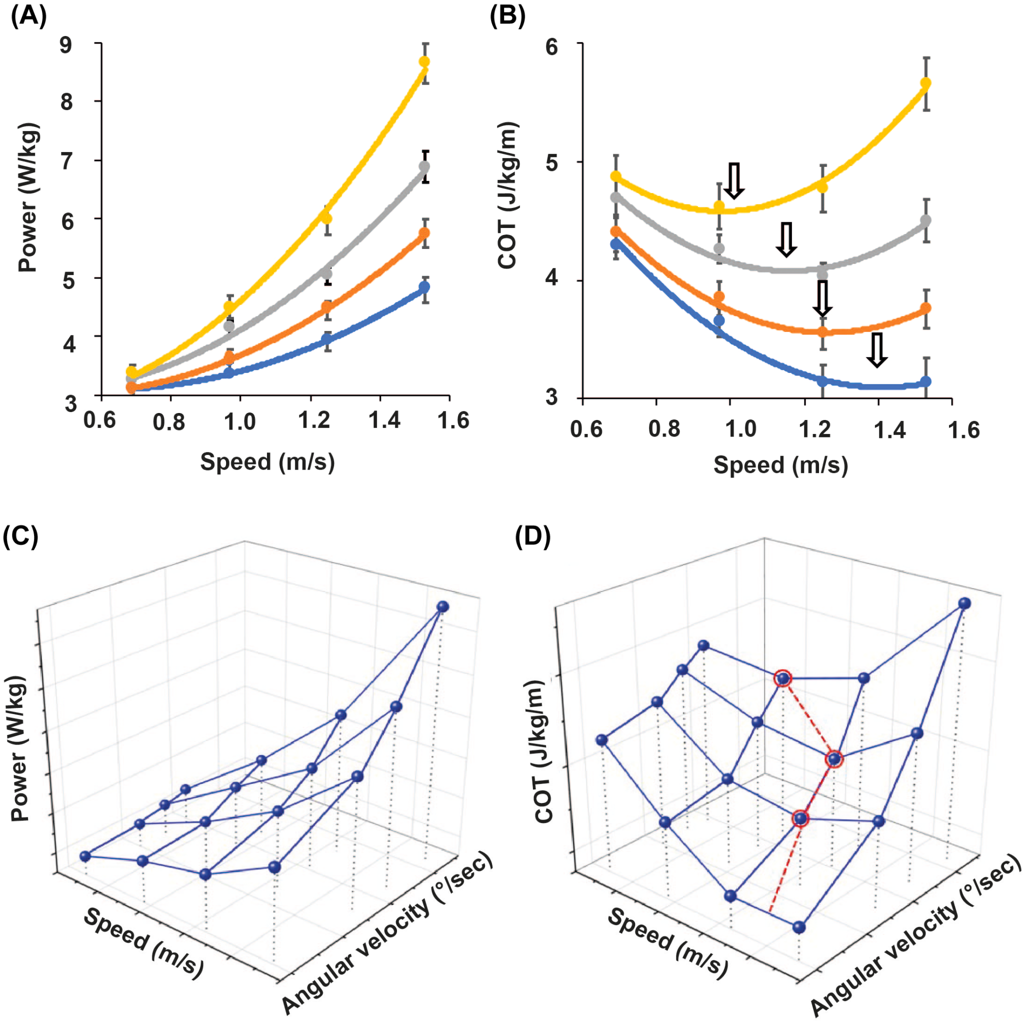

Figure 1. Metabolic measurements versus average travel speed or both travel speed and angular velocity for 20 human participants walking tracks with turns of varied extent. (A) Mean (± SE) total mass-specific power and (B) mean (± SE) total mass-specific cost of transport for straight movement (blue), 90° turns every 5 m (orange), 135° turns every 5 m (grey) and a 180° turns every 5 m (yellow). Quadratic curves were fitted using the coefficients of the outputs of linear mixed-effects models (Table 1). Arrows show COT_{min} speeds. (C) and (D) are 3D plots of the same data including angular velocity as a covariate. The accelerating power costs of higher angular velocities produce cost of transit minima (highlighted in red) where any turning occurs and these minima occur at lower speeds with higher angular velocities.

Table 2. Summary of the outputs of linear mixed-effects models conducted to investigate the effects of speed and angle on angular velocity or metabolic parameters and the effects of speed and angular velocity on metabolic parameters.

Parameter	Term	F	df	p	R^2 Fixed factors	R^2 total model	Coefficients
Angular velocity (° s^{-1})	U	1037.87	1,289	< 0.001	0.979	0.983	0°: $=0U+0$
	angle [as factor]	5365.33	3,289	< 0.001			90°: $=31.94U+28.07$
	U: angle [as factor]	170.86	3,289	< 0.001			135°: $=46.60U+43.28$
							180°: $=73.5\ U+43.92$
Angular velocity (° s^{-1})	angle	16001.97	1,289	< 0.001	0.979	0.982	0.69 m s^{-1}: $=0.54$(angle)$+0.89$
	U [as factor]	345.09	3,289	< 0.001			0.97 m s^{-1}: $=0.64$(angle)$+0.38$
	angle: U [as factor]	168.49	3,289	< 0.001			1.25 m s^{-1}: $=0.74$(angle)$+0.86$
							1.53 m s^{-1}: $=0.88$(angle) $-$ 1.10
P_{met} (W kg^{-1})	U	9.37	1,284	0.002	0.769	0.919	0°: $=1.99$(speed)^2 $-$ 2.39(speed)$+3.80$
	U^2	65.29	1,284	< 0.001			90°: $=2.48$(speed)^2 $-$ 2.39(speed)$+3.59$
	angle [as factor]	201.83	3,284	< 0.001			135°: $=2.97$(speed)^2 $-$ 2.39(speed)$+3.53$
	U^2: angle [as factor]	101.81	3,284	< 0.001			180°: $=3.87$(speed)^2 $-$ 2.39(speed)$+3.13$
CoT (J kg^{-1} m^{-1})	U	137.17	1,284	< 0.001	0.471	0.860	0°: $=2.38$(speed)^2 $-$ 6.71(speed)$+7.83$
	U^2	122.52	1,284	< 0.001			90°: $=2.66$(speed)^2 $-$ 6.71(speed)$+7.80$
	angle [as factor]	234.82	3,284	< 0.001			135°: $=2.90$(speed)^2 $-$ 6.71(speed)$+7.97$
	U^2: angle [as factor]	59.13	3,284	< 0.001			180°: $=3.43$(speed)^2 $-$ 6.71(speed)$+7.86$
Turn cost (J kg^{-1})	U	1.58	1,203	0.209	0.658	0.770	90°: $=3.46$(speed)^2 $-$ 4.66(speed)$+2.29$
	U^2	9.73	1,203	0.002			135°: $=4.70$(speed)^2 $-$ 4.66(speed)$+2.99$
	angle [as factor]	147.09	2,203	< 0.001			180°: $=7.34$(speed)^2 $-$ 4.66(speed)$+2.56$
	U^2: angle [as factor]	37.98	2,203	< 0.001			
Turn P_{met} (W kg^{-1})	U	7.77	1,203	0.006	0.739	0.814	90°: $=4.73$(speed)^2 $-$ 7.79(speed)$+3.62$
	U^2	26.60	1,203	< 0.001			135°: $=6.00$(speed)^2 $-$ 7.79(speed)$+3.71$
	angle [as factor]	154.09	2,203	< 0.001			180°: $=8.62$(speed)^2 $-$ 7.79(speed)$+2.64$
	U^2: angle [as factor]	66.87	2,203	< 0.001			
Turn cost (J kg^{-1})	*Angular velocity*	1.87	1,284	0.285	0.711	0.770	0.69 m s^{-1}: 0.0002(angular velocity)^2$+$0.0079(angular velocity) $-$ 0.0686
	Angle [as factor]^2	13.67	1,282	< 0.001			0.97 m s^{-1}: 0.0003(angular velocity)^2$+$0.0079(angular velocity) $-$ 0.2339
	U [as factor]	5.66	2,280	< 0.001			1.25 m s^{-1}: 0.0004(angular velocity)^2$+$0.0079(angular velocity) $-$ 0.1453
	Angle [as factor]^2: U [as factor]	3.49	2,280	0.016			1.53 m s^{-1}: 0.0004(angular velocity)^2$+$0.0079(angular velocity) $-$ 0.2471
Turn P_{met} (W kg^{-1})	*Angular velocity*	0.80	1,204	0.371	0.734	0.817	0.69 m s^{-1}: 0.0002(angular velocity)^2$+$0.0018(angular velocity) $-$ 0.0334
	Angle [as factor]^2	46.83	1,204	< 0.001			0.97 m s^{-1}: 0.0002(angular velocity)^2$+$0.0018(angular velocity) $-$ 0.1211
	U [as factor]	21.46	3,204	< 0.001			1.25 m s^{-1}: 0.0003(angular velocity)^2$+$0.0018(angular velocity) $-$ 0.0595
	Angle [as factor]^2: U [as factor]	3.75	3,204	0.011			1.53 m s^{-1}: 0.0004(angular velocity)^2$+$0.0018(angular velocity) $-$ 0.1199

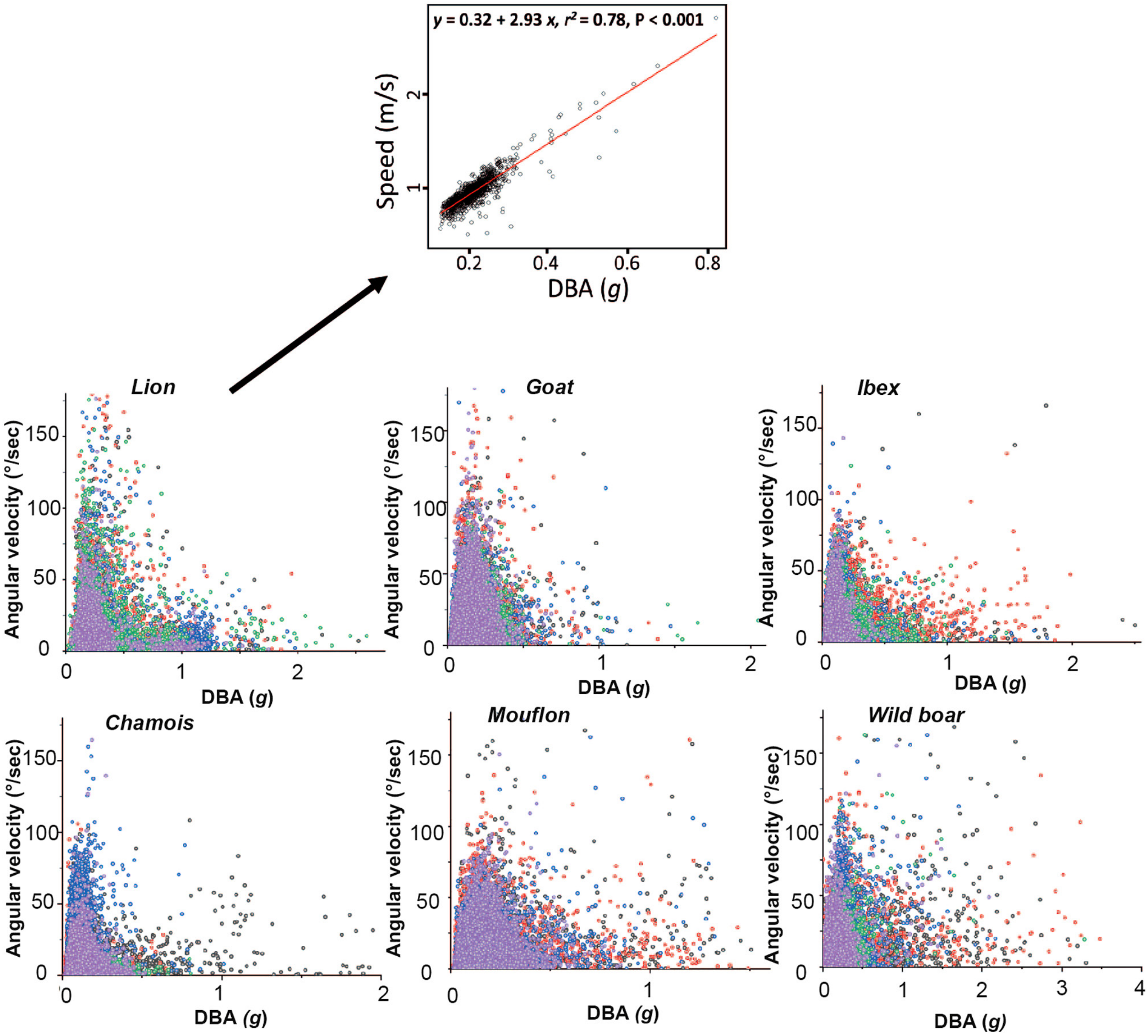

Figure 2. Incidence of angular velocity against dynamic body acceleration (DBA) – a linear proxy for travel speed – in six free-living terrestrial species. The lion data shows an inset that clarifies the relationship between DBA and speed for this species, these animals being equipped with GPS recording at 1 Hz. Each point shows a value taken at ca 10 s intervals over a length of time that corresponds to about 20 000 points for each individual ($n = 5$ per species except for the mouflon where $n = 4$, with individuals depicted by different colors – the predominance of purple simply reflects data from the last individual graphed by the package). Note how all distributions show decreasing angular velocities with increasing speed across all speed ranges, starting with the slowest.

minimum costs of transport occurred at lower walking speeds when angular velocities were high (Fig. 1c–d).

Similarly, significant effects of interaction terms were found for the quadratic relationships between speed and cost per turn (J kg^{-1}, $speed^2 \times$ angle category, $F = 37.98$, $p < 0.001$) and turn power (W kg^{-1}, $speed^2 \times$ angle category, $F = 66.87$, $p < 0.001$) with the rate of increase of power with speed becoming greater as angle increased (Table 2).

Wild animal data support the idea that preferred travel speed decreases with increasing angular velocity

In free-ranging wild mammal species (African lions *Pathera leo*, chamois *Capra rubicapra*, ibex *Capra ibex*, mouflon *Ovis orientalis*, wild boar *Sus scrofa*) and one domestic animal (the goat *Capra aegagrus*), all individuals tended to travel relatively slowly, but they predominantly engaged in the highest angular velocities at the lowest travel speeds (using dynamic body acceleration as a proxy for speed (Bidder et al. 2012b)) decreasing angular velocities in their turns as their travel speeds increased (Fig. 2). The incidence of turning behavior was apparent in examples of the free-living animal movement data when resolved at sub-second level, which showed intensive and extensive turning behavior, even when movement paths appeared directed at larger scales (Fig. 3).

Discussion

There have been extensive studies of the relationship between terrestrial animal speed and power, the vast majority of which have been conducted on a treadmill to show that power increases linearly with speed (Taylor et al. 1970).

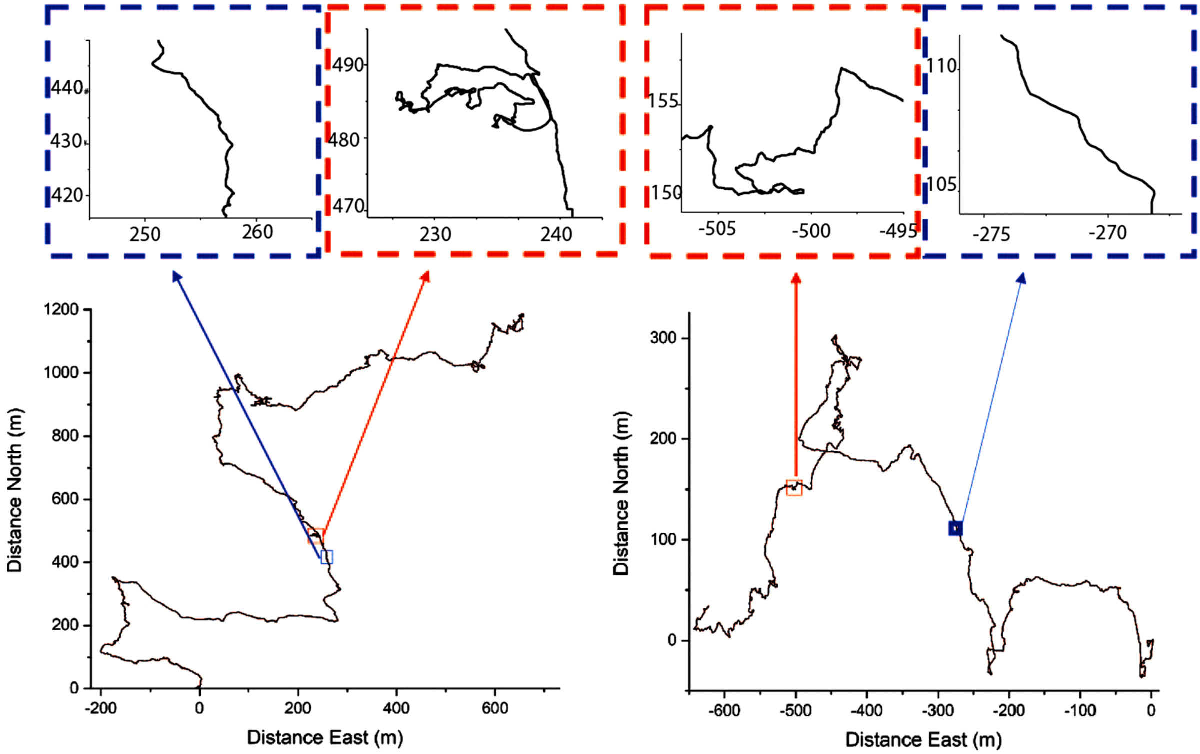

Figure 3. Examples of 20 h movement paths (at 4 Hz and elucidated by dead-reckoning) of two of the study animals. (A) a chamois and (B) an ibex, showing in the insets the scale over which turns are made (cf. our VO_2 study on humans). Note how even apparently straight-line paths (blue boxes) show clear turns, although angles are obtuse, while tortuous sections (red boxes) show both obtuse and acute turns.

While fundamental, this highly controlled scenario does not simulate the situation found in nature where variability in, for example, topography and surface penetrability of the environment will also affect power to travel (Shepard et al. 2013) and thereby the cost of transport. Interestingly, in a recent study of how scaling affects costs in animals moving on inclines, Halsey and White (2017) present data that show clear minima in costs of transport with slope (although the effect of speed is not detailed). This, therefore, already points to an important effect of how the environment is expected to structure selection of animal speed for energetically optimum movement. But beyond this, animals may turn to avoid energetically onerous landscape features such as inclines (Shepard et al. 2013) and, for this and for many other reasons, they turn frequently, as our Fig. 3 shows. Previous works have indicated that turns are energetically costly (Wilson et al. 2013, McNarry et al. 2017) but, due to their experimental protocol, these authors could not define how the costs of transport relate to angular velocity and speed, nor that angular velocity could have created clear minima in costs of transport at such low speeds. The extraordinary magnitude of the increase in power costs with increasing angular velocity and speed is, in part, explained by animals having to develop forces to counteract the centripetal force incurred in the turn, given by; $F = m \times v^2/r$, where m is the mass, v, the velocity and r the radius of the turn. Thus, some of the energy used for turning has to be used in developing lateral forces. However, acute turns will also require some forces opposing the drive force, manifesting as deceleration followed by corrective acceleration for straight-line travel after a turn. This will occur even at low speeds, which explains the sharp drop off in angular velocity in turns, even at low speeds in our wild animals (Fig. 2), and the minimum cost of transport occurring at such low walking speeds of humans during 180° turns (Fig. 1). Indeed, application of the COT_{min} travel speeds for straight line paths in humans to our scenario with 180° turns would incur a predicted increase of 13% in travel costs above the angle-specific COT_{min} (cf. Fig. 1b). We note that the specifics of the power- and COT values for humans, with their bipedal inverted pendulum locomotion (Kuo et al. 2005), are unlikely to translate directly to quadrupeds, particularly given the variation in locomotory morphologies within this group (Steudel 1990, Pontzer 2007) but the physical principles are the same so the general patterns observed for humans should be apparent in wild animals to a greater or lesser degree.

The high power associated with turns translates into well-defined minima in the costs of transport for defined speeds and angular velocities (Fig. 1d). This means that an overall optimum speed for a wild animal, moving to minimize transport costs, will depend on the frequency and extent of turns. These will depend on a large number of turn elicitors that confer benefit to the animal if it turns. These, in turn, will range from barriers, including localized ones such as trees/shrubs (Schooley et al. 1996), or navigating through differential energy landscapes (Shepard et al. 2013), through to acquisition strategies for food, such as area-restricted search

(Walsh 1996), or mates (Bau and Carde 2015). Indeed, we suggest that the incidence of turning behavior in wild animals has been underestimated, not least because we have little capacity to resolve it at the scale necessary to be energetically meaningful, even using GPS technology (Hulbert and French 2001). A notable exception is with inertial/dead-reckoned data (Bidder et al. 2015), which show that animal paths can consist of extensive and intensive turning behavior (Fig. 3).

Variation in the environment or in animal behavior would also lead us to expect animals to vary travel speed accordingly, even intra-specifically, reflecting different motivations for speed selection (Wilson et al. 2015), which is consistent with the animal data we present here (Fig. 3). Clearly, although such data may not always agree with animals actually using COT_{min} for a number of reasons (Wilson et al. 2015), the interplay of speed and angular velocity, and the huge effect that they have on movement energetics, points to the importance of both in modulating trajectories according to function. Indeed, future treatises that attempt to link this with the multiple other factors that affect the energy costs of travel (e.g. the energy landscape (Shepard et al. 2013)) may find that we can explain animal speed- and turn velocity-selection more satisfactorily than we can at present.

Our treatment is simplistic for a number of reasons. Not least, we only consider power and COT metrics as bi-dimensional when they will be affected by multiple properties of the environment that modulate power use, such as slope and surface penetrability (Shepard et al. 2013). This will be further complicated by gait changes (Dawson and Taylor 1973, Maloiy et al. 2009, Nudds et al. 2011, Watson et al. 2011, Granatosky et al. 2018). This work nevertheless demonstrates the profound effect that turns have on cost of transport for terrestrial animals using humans as a model, although we expect the principle to be the same for flying and aquatic animals. If we are to progress with models purporting to help us understand animal trajectories through varying environmental space from an energetic, and ultimately behavioral, perspective though, we will have to accept that small things such as acute corners can sometimes make big differences in understanding the details and elicitors of movement trajectories (Schick et al. 2008).

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Author contributions

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