

## Reappraisal of the comparative cost of human locomotion using gait-specific allometric analyses

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### Summary

The alleged high net energy cost of running and low net energy cost of walking in humans have played an important role in the interpretation of the evolution of human bipedalism and the biomechanical determinants of the metabolic cost of locomotion. This study re-explores how the net metabolic energy cost of running and walking ( $\text{J kg}^{-1} \text{m}^{-1}$ ) in humans compares to that of animals of similar mass using new allometric analyses of previously published data. Firstly, this study shows that the use of the slope of the regression between the rate of energy expenditure and speed to calculate the net energy cost of locomotion overestimates the net cost of human running. Also, the net energy cost of human running is only 17% higher than that predicted based on their mass. This value is not exceptional given that over a quarter of the previously examined mammals and birds have a net energy

cost of running that is 17% or more above their allometrically predicted value. Using a new allometric equation for the net energy cost of walking, this study also shows that human walking is 20% less expensive than predicted for their mass. Of the animals used to generate this equation, 25% have a relatively lower net cost of walking compared with their allometrically predicted value. This new walking allometric analysis also indicates that the scaling of the net energy cost of locomotion with body mass is gait dependent. In conclusion, the net costs of running and walking in humans are moderately different from those predicted from allometry and are not remarkable for an animal of its size.

Key words: cost of locomotion, human, metabolism, walk, run, bipedalism, allometry.

### Introduction

There is much interest in the comparative cost of human bipedal locomotion. Since the pioneering work of C. R. Taylor and colleagues (Taylor et al., 1970), it has generally been acknowledged that the net cost of running ( $E_{\text{run}}$ ;  $\text{J kg}^{-1} \text{m}^{-1}$ ) in humans is considerably higher than predicted for an animal of a similar mass (Schmidt-Nielsen, 1975; Rodman and McHenry, 1980; Carrier, 1984; Taylor, 1994; Steudel, 1996; Leonard and Robertson, 1997; Aiello and Wells, 2002; Steudel-Numbers, 2003; Bramble and Lieberman, 2004). At the origin of this view is the allometric analysis of  $E_{\text{run}}$  in humans and other mammalian species performed by Taylor et al. (Taylor et al., 1970), where  $E_{\text{run}}$  in humans was shown to be twice (100% greater) than predicted for an animal of the same mass. Later work by the same research group, aimed at elucidating more precisely the scaling relationship of  $E_{\text{run}}$ , incorporated a large amount of data from several taxonomic groups (Taylor et al., 1982) and reported human  $E_{\text{run}}$  to be ~43% greater than predicted allometrically. It was also established in this study and the study of Fedak and Seeherman (Fedak and Seeherman, 1979) that the high cost of human running is not typical of

bipedalism, since the cost of running in quadrupeds was found to be similar to that of bipeds.

These findings on the energy cost of human running have had important consequences for our understanding of human locomotion. Anthropologists, human biologists, ecologists and evolutionary theorists have often based their interpretations of the evolution of human bipedalism and the adaptive value of human locomotion on the studies of Taylor and colleagues (Taylor et al., 1970; Taylor et al., 1982) and have generated an impressive volume of studies in these areas (e.g. Rodman and McHenry, 1980; Carrier, 1984; Leonard and Robertson, 1997; Steudel-Numbers, 2001; Aiello and Wells, 2002; Bramble and Lieberman, 2004). The comparison of running costs between humans and other animal species has also been important for vertebrate morphologists, physiologists and biomechanists attempting to understand structure–function relationships amongst limbed vertebrates (Roberts et al., 1998).

One major limitation shared by most of the aforementioned studies addressing the biological significance of human  $E_{\text{run}}$  is that they have overlooked that the analyses of Taylor et al. (Taylor et al., 1970; Taylor et al., 1982) on which their interpretations are

based were aimed at understanding how  $E_{\text{run}}$  scales with body mass rather than to specifically compare human  $E_{\text{run}}$  with those of other species. Because Taylor and colleagues were not interested in humans *per se*, their studies relied on data from a relatively small number of human studies. Although this is suitable for allometry studies involving a large number of species, the use of human data from only a small number of studies may not represent accurately the 'average'  $E_{\text{run}}$  of humans since human  $E_{\text{run}}$  varies substantially between individuals and across studies (Daniels, 1985). This is highlighted in a more recent allometry study on bipedal species (Roberts et al., 1998), where the  $E_{\text{run}}$  of a group of human subjects did not differ from the allometrically predicted value. This result is due to the  $E_{\text{run}}$  of their human subjects being among the lowest found in the literature. Another difficulty with comparing human  $E_{\text{run}}$  with that predicted from allometry is that  $E_{\text{run}}$  in allometric analyses is generally calculated from the slope of the linear relationship between the rate of energy expenditure ( $\dot{E}_{\text{met}}$ ;  $\text{W kg}^{-1}$ ) and speed. The limitation with this approach is that for the slope of  $\dot{E}_{\text{met}}$  versus speed to be a valid measure of  $E_{\text{run}}$ , the y-intercept must coincide with the non-locomotor metabolic rate. Although a mismatch between the y-intercept and the non-locomotor metabolic rate is likely to have only a minor effect in allometric analyses of  $E_{\text{run}}$  based on a large

number of animal species, such a mismatch in humans could affect significantly any estimate of their  $E_{\text{run}}$  relative to other species. Finally, another factor that has the potential to affect the comparison of  $E_{\text{run}}$  of humans with that predicted from allometric analyses is the fact that most previous allometry studies have been compiled from data in a manner that does not specifically distinguish between walking and running gaits, a potential difficulty given that walking and running elicit different costs of locomotion (Margaria et al., 1963; Minetti et al., 1999).

Given these difficulties shared by the studies using the findings of Taylor and colleagues (Taylor et al., 1970; Taylor et al., 1982) to compare  $E_{\text{run}}$  between humans and other species, the first aim of the present study was to examine specifically if humans have an atypically high net cost of running, relative to their mass, compared to other animal species. To this end, we used an allometric analysis that assesses how the  $E_{\text{run}}$  of humans compares to the predicted  $E_{\text{run}}$  for animals of similar mass not only by making a more extensive use of the human data available from the literature but also by adopting a more appropriate method of subtracting the experimental non-locomotor cost from the gross metabolic cost of locomotion and by restricting our analysis to studies where the net cost of locomotion can be determined specifically for running.

Table 1. Human data (means) of net energy cost of running taken from the literature, used to compare with allometric predictions

(A) Slope method			(B) Subtraction method		
Mass (kg)	$E_{\text{run}}$ (net) ( $\text{J kg}^{-1} \text{m}^{-1}$ )	Reference	Mass (kg)	$E_{\text{run}}$ (net) ( $\text{J kg}^{-1} \text{m}^{-1}$ )	Reference
70.1	3.92	(Boje, 1944)	72.7	3.15	(Bergh et al., 1991) BA
53.7	3.66	(Bransford and Howley, 1977) FT	66.5	3.29	(Bergh et al., 1991) MR
59.8	3.04	(Bransford and Howley, 1977) FU	51.7	3.61	(Bergh et al., 1991) FR
67.0	4.08	(Bransford and Howley, 1977) MT	72.3	3.14	(Bergh et al., 1991) SO
80.2	4.10	(Bransford and Howley, 1977) MU	70.1	3.75	(Boje, 1944)
64.6	4.20	(Conley and Krahenbuhl, 1980)	53.7	3.56	(Bransford and Howley, 1977) FT
63.1	4.19	(Costill and Fox, 1969)	59.8	3.51	(Bransford and Howley, 1977) FU
63.7	5.07	(Costill et al., 1973)	67.0	3.43	(Bransford and Howley, 1977) MT
65.4	4.82	(Daniels and Daniels, 1992)	80.2	3.57	(Bransford and Howley, 1977) MU
58.9	4.24	(Daniels et al., 1977)	64.6	3.44	(Conley and Krahenbuhl, 1980)
65.1	3.18	(Dressendorfer et al., 1977)	63.1	3.42	(Costill and Fox, 1969)
65.4	4.70	(Hagan et al., 1980)	63.7	3.56	(Costill et al., 1973)
73.8	4.18	(Knuttgen, 1961)	65.4	3.49	(Daniels and Daniels, 1992)
68.8	4.02	(Margaria et al., 1963)	58.9	3.39	(Daniels et al., 1977)
67.5	4.19	(Mayhew, 1977)	65.1	3.31	(Dressendorfer et al., 1977)
66.1	3.46	(Mckicken and Daniels, 1976)	65.4	4.48	(Hagan et al., 1980)
69.9	3.77	(Menier and Pugh, 1968)	73.8	3.82	(Knuttgen, 1961)
61.4	3.59	(Pugh, 1971)	68.8	4.23	(Margaria et al., 1963)
78.8	2.75	(Roberts et al., 1998)	67.5	3.59	(Mayhew, 1977)
66.4	3.99	(Saunders et al., 2004a)	66.1	3.54	(Mckicken and Daniels, 1976)
65.7	4.63	(Saunders et al., 2004b)	69.9	3.45	(Menier and Pugh, 1968)
70.0	3.46	(Sheppard, 1969)	61.4	3.24	(Pugh, 1971)
70.0	2.94	(Wright and Weyand, 2001)	66.4	3.48	(Saunders et al., 2004a)
			65.7	3.77	(Saunders et al., 2004b)
			70.0	3.73	(Sheppard, 1969)
			70.0	3.22	(Wright and Weyand, 2001)
Mean			Mean		
66.8	3.92		66.1	3.55	

(A) Net energy cost of running calculated using the slope method. (B) Net energy cost of running calculated using the subtraction method.

For studies where multiple values exist, symbols represent groups: BA (biathletes), MR (male runners), FR (female runners), SO (ski orienteers), FT (female trained), FU (female untrained), MT (male trained), MU (male untrained).

Our second aim follows from the observation that it is also unclear how the metabolic cost of walking in humans compares to that of other species, with some authors claiming that humans' cost of walking is lower than that of animals of similar mass (Studel, 1996; Studel-Numbers, 2003) while others claim that it is similar (Rodman and McHenry, 1980; Alexander, 1991; Alexander, 1992). Given that the comparative cost of human walking also has important biological and evolutionary significance (Alexander, 1991; Studel, 1996; Leonard and Robertson, 1997; Studel-Numbers, 2003), it was our objective to address this controversy by extending our analyses to specifically compare the net cost of walking ( $E_{\text{walk}}$ ;  $\text{J kg}^{-1} \text{m}^{-1}$ ) between humans and other species.

**Materials and methods**

*Comparison of human net metabolic cost of running and walking from literature*

Published mean values of human metabolic energy costs of running from 20 sources (Table 1A,B) were compared to the metabolic energy cost of transport obtained from the allometric equation of Taylor et al. (Taylor et al., 1982):

$$E_{\text{run}} = 10.7 M_b^{-0.316}, \quad (1)$$

where  $M_b$  is body mass in kg and  $E_{\text{run}}$  is in  $\text{J kg}^{-1} \text{m}^{-1}$ . Published human values were compared to this equation in two ways. The first approach calculates  $E_{\text{run}}$  from the slope of the linear regression between the gross mass-specific rate of energy expenditure ( $\dot{E}_{\text{met}}$ ;  $\text{W kg}^{-1}$ ) and speed (slope method) (Table 1A). This approach has traditionally been used to represent  $E_{\text{run}}$  (Taylor et al., 1970; Full, 1991) and has the benefit of providing a single value for  $E_{\text{run}}$ . However, it assumes that the y-intercept of the linear regression between  $\dot{E}_{\text{met}}$  and speed approximates the non-locomotor metabolic rate. The second approach calculates  $E_{\text{run}}$  by subtracting the measured non-locomotor metabolic rate from the gross metabolic rate at a given speed and dividing by that speed (subtraction method) (Table 1B). This latter approach assumes that the subtracted non-locomotor cost remains the same across exercise intensity. Although changes in energy use by non-locomotor tissues occur, studies on both humans and other animals indicate that these changes are small or negligible compared to the altered energy use by limb muscles (Poole et al., 1992; Musch et al., 2004; Ellerby et al., 2005; Marsh and Ellerby, 2006).

Gross metabolic rates were obtained either from published regression equations or from single (mean) published values. For studies where only rates of oxygen consumption were presented, energy expenditure was calculated using an energy equivalent of  $20.1 \text{ J ml}^{-1} \text{ O}_2$ . Non-locomotor metabolic rates in humans were either published values of standing metabolic rate or, when unavailable, assumed to be equal to  $1.5 \text{ W kg}^{-1}$ , a representative value based on data from the literature (Burdett et al., 1983; Farley and McMahon, 1992; Martin et al., 1992; Waters and Mulroy, 1999; Bastien et al., 2005; Browning et al., 2006). Because  $E_{\text{run}}$  calculated using the subtraction method has no unique value over a range of speeds, calculations were made close to the middle of the speed range examined in each study (these were generally between  $3.0$  and  $4.5 \text{ m s}^{-1}$ , common speeds for recreational runners).

Since differences in  $E_{\text{run}}$  based on these two approaches (slope method and subtraction method) may also be present in other species, it is possible that they also affect the scaling relationship of  $E_{\text{run}}$  and body mass. For this reason, we have also generated a new allometric equation for  $E_{\text{run}}$  from existing data from studies where both experimental values of non-locomotor metabolic rates and gross running metabolic rates are provided (Table 3). Our analyses included 17 of the 95 animals in the data set of Taylor et al. (Taylor et al., 1982) and 14 additional species from other studies. Calculations were made close to the middle of the speed range of each animal examined. In order to ensure further that the selected animals were running over the targeted speed range, gait criteria were either based on existing published reports on gait mechanics (e.g. Cavagna et al., 1977; Fedak et al., 1982; Gatesy and Biewener, 1991) or an estimate of the animals' Froude number (see Alexander, 1989). The transition from walking to running has generally been found to occur at a Froude number of approximately 0.5 in a large range of vertebrate species (Alexander, 1989; Kram et al., 1997). We only accepted conservative values (above 0.6 for running). The allometric equation developed from these data provided a means to compare human net cost of running using the subtraction method with an allometrically predicted value of  $E_{\text{run}}$  based on the same approach.

A new allometric relationship between the net minimum energy cost of walking and body mass was also constructed based on the subtraction method. Our analysis focused on the minimum net cost of walking because  $E_{\text{walk}}$  is speed-dependent in certain species [e.g. humans (Margaria, 1976); horses (Minetti et al., 1999)]. We performed one analysis that included only those

Table 2. Human data (means) of net energy cost of walking taken from the literature, used to compare with allometric predictions

Mass (kg)	$E_{\text{walk}}$ (net) ( $\text{J kg}^{-1} \text{m}^{-1}$ )	Reference
67.0	1.91	(Bastien et al., 2005)
56.8	2.45	(Booyens and Keatinge, 1957)
58.7	1.98	(Browning and Kram, 2005)
74.7	1.80	(Browning et al., 2006)
65.2	2.31	(Burdett et al., 1983)
59.0	1.91	(Dolgener, 1982)
70.4	2.59	(Duggan and Haisman, 1992)
65.0	2.12	(Farley and McMahon, 1992)
66.7	2.00	(Gottschall and Kram, 2003)
70.8	2.06	(Howley and Glover, 1974)
63.2	2.22	(Martin et al., 1992)
72.0	2.15	(McCann and Williams, 2002)
84.1	2.15	(Minetti et al., 1995)
66.1	1.80	(Ortega and Farley, 2005)
76.3	1.71	(Pearce et al., 1983)
76.0	2.37	(Ralston, 1958)
75.8	2.24	(van der Walt and Wyndham, 1973)
72.8	1.91	(Waters et al., 1988)
70.0	1.86	(Waters et al., 1983)
80.0	1.77	(Yousef et al., 1989)
Mean		
69.5	2.06	

Values were calculated using the subtraction method.

studies where an estimate of minimum  $E_{\text{walk}}$  could be provided from the  $E_{\text{walk}}$  determined over a range of walking speeds (denoted  $E_{\text{walk,min}}$ ). In addition, we performed an analysis that also included  $E_{\text{walk}}$  of species determined at a self-selected speed, since these speeds are thought to coincide with the minimum  $E_{\text{walk}}$  speed (Hoyt and Taylor, 1981). Because the fraction of the non-locomotor rate of energy expenditure accounts for a greater percentage of the exercising metabolic rate during walking compared to running, all studies selected for our allometric analyses had to provide a measurement of standing metabolic rate. Finally, in order to ensure further that the animals selected for our study were actually walking, walking gait criteria were based either on previously published reports on gait mechanics in the animal under consideration (e.g. Gatesy and Biewener, 1991; Cavagna et al., 1977; Fedak et al., 1982) or, where gait mechanics were not available, on an estimate of the animal's Froude number at the speed being examined. Only speeds where the Froude

number was below 0.4 were included. Metabolic rates presented as rates of oxygen consumption were converted to a rate of energy expenditure as described above. Because of the strict criteria set for our walking allometry, a large body of literature reporting walking metabolic rates in animals had to be excluded, and for this reason our analysis included 21 species of mammals and birds ranging in mass from 300 g to 1500 kg (see Table 4). Finally, the minimum net energy costs of human walking (at speeds approximating  $1.25 \text{ m s}^{-1}$ ) were taken from 20 previously published sources (Table 2) and calculated as described above for  $E_{\text{run}}$ .

#### Statistical analysis

In order to determine whether the slope and subtraction methods for calculating  $E_{\text{run}}$  yield significantly different allometric relationships, we first tabulated the data from Taylor et al. (Taylor et al., 1982) and included in our analysis those

Table 3. Data from the literature used to construct the allometric equation (Eqn 2) for the net energy cost of running based on the subtraction method

Animal	Mass (kg)	$E_{\text{run}}$ (net) ( $\text{J kg}^{-1} \text{ m}^{-1}$ )	Non-locomotor cost ( $\text{W kg}^{-1}$ )	Speed ( $\text{m s}^{-1}$ )	Reference
<b>Mammals</b>					
White mouse	0.021	85.56	12.67	0.21	(Taylor et al., 1970)
Deer mouse	0.022	65.08	8.25	0.56	(Chappel et al., 2004)
Kangaroo rat*	0.041	45.23	8.43	0.28	(Taylor et al., 1970)
Merriam's chipmunk	0.075	36.10	8.21	0.67	(Wundur, 1970)
Kangaroo rat†	0.100	31.69	6.37	0.42	(Taylor et al., 1970)
Ground squirrel	0.236	14.67	6.31	0.56	(Taylor et al., 1970)
Red squirrel	0.252	17.80	12.06	0.58	(Wunder and Morrison, 1974)
White rat	0.384	27.19	5.67	0.49	(Taylor et al., 1970)
Bettong rat kangaroo	0.97	10.85	2.61	4.00	(Webster and Dawson, 2003)
Brush-tailed possum	1.95	11.38	4.41	1.49	(Baudinette et al., 1978)
Mongrel dog	2.6	7.24	3.40	1.94	(Taylor et al., 1970)
Patas monkey	3.8	6.29	3.00	3.47	(Mahoney, 1980)
Tammar wallaby	4.68	4.29	1.94	4.50	(Baudinette et al., 1987)
Hunting dog	8.75	6.17	4.07	2.78	(Taylor et al., 1971a)
River otter	11.1	6.71	3.34	1.40	(Williams et al., 2002)
Walker foxhound	18.0	4.36	1.79	1.94	(Taylor et al., 1970)
Elk calf	50.0	4.30	2.74	2.22	(Cohen et al., 1978)
Human	66.1	3.55	1.5	3.0–4.5	Mean data (see Table 1B)
Miniature horse	121	2.07	1.34	1.70	(Griffin et al., 2004), T. M. Griffin (personal communication)
Shetland pony	140	1.72	1.35	3.06	(Hoyt and Taylor, 1981), D. F. Hoyt (personal communication)
Arabian horse	448	1.63	1.29	2.70	(Griffin et al., 2004), T. M. Griffin (personal communication)
Camel	477	1.33	0.54	6.00	(Evans et al., 1994)
Standardbred horse	515	1.98	0.65	3.50	(Minetti et al., 1999)
Draft horse	715	1.93	1.38	3.00	(Griffin et al., 2004), T. M. Griffin (personal communication)
<b>Birds</b>					
Painted quail	0.042	26.63	11.61	0.56	(Fedak et al., 1974)
Bob-white quail	0.194	18.57	7.48	0.69	(Fedak et al., 1974)
Chuckar partridge	0.489	14.74	7.54	0.83	(Fedak et al., 1974)
Guinea fowl	1.45	9.14	6.37	2.50	(Ellerby et al., 2003)
Wild turkey	4.31	8.47	3.13	2.22	(Fedak et al., 1974)
Rhea	22.0	6.85	2.12	2.78	(Taylor et al., 1971b)
Ostrich	66.1	2.45	1.81	2.5–4.0‡	(Rubenson et al., 2004)

\**Dipodomys merriami*. †*Dipodomys spectabilis*. ‡The mean  $E_{\text{run}}$  over the running speed range is used.

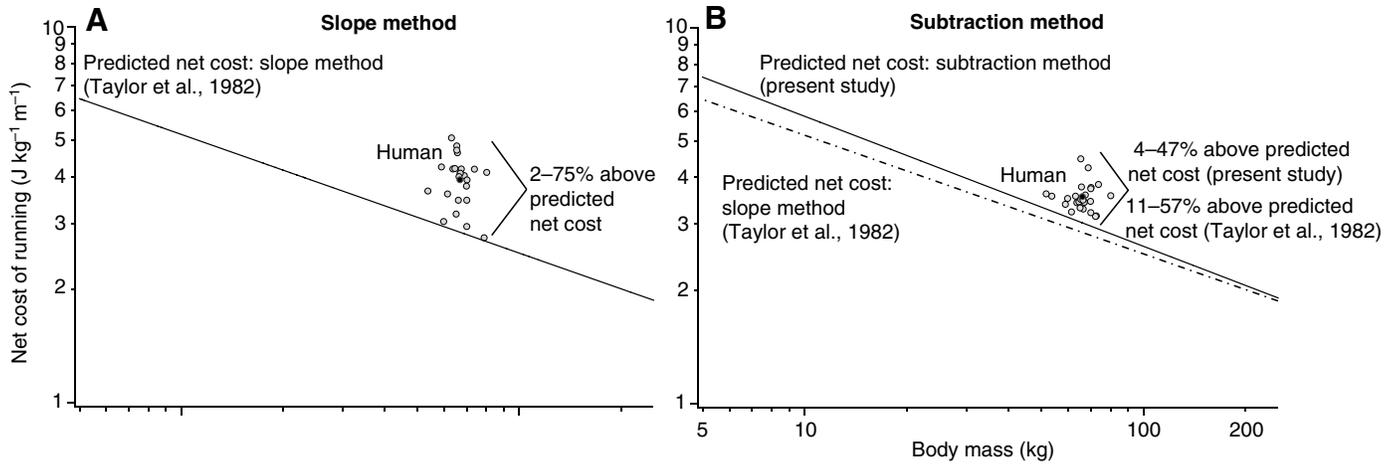


Fig. 1. Double logarithmic plot of the net energy cost of human running ( $E_{run}$ ) versus body mass calculated from the slope method (A) and subtraction method (B) (see Materials and methods for explanation). The shaded circles represent human data from 20 previously published sources (see Table 1A and Table 1B for corresponding data), and the solid circle represents the mean value from these studies. The solid line in A and the broken line in B correspond to  $E_{run}$  predicted from the allometric equation of Taylor et al. (Taylor et al., 1982) (Eqn 1). The solid line in B corresponds to  $E_{run}$  predicted from the new allometric equation from the present study (Eqn 2).

animals that were used to develop their allometric equation ( $N=89$ ). We estimated a regression with  $E_{run}$  (log-transformed) from both Taylor et al. (Taylor et al., 1982) and our new data set (Table 3) as the dependent variable, a categorical variable for the slope or subtraction method as a fixed factor, and body mass (log-transformed) as a covariate (General Linear Model using SPSS version 13). We also performed a similar analysis on log-transformed data to determine whether the allometric relationship of the net cost of locomotion is different for running and walking gaits. We used cost ( $E_{run}$  and  $E_{walk}$ ) as the dependent variable, a categorical variable for gait (walking vs running) as a fixed factor, and body mass as a covariate. Main and interaction effects were analyzed at a significance level of  $P < 0.05$ .

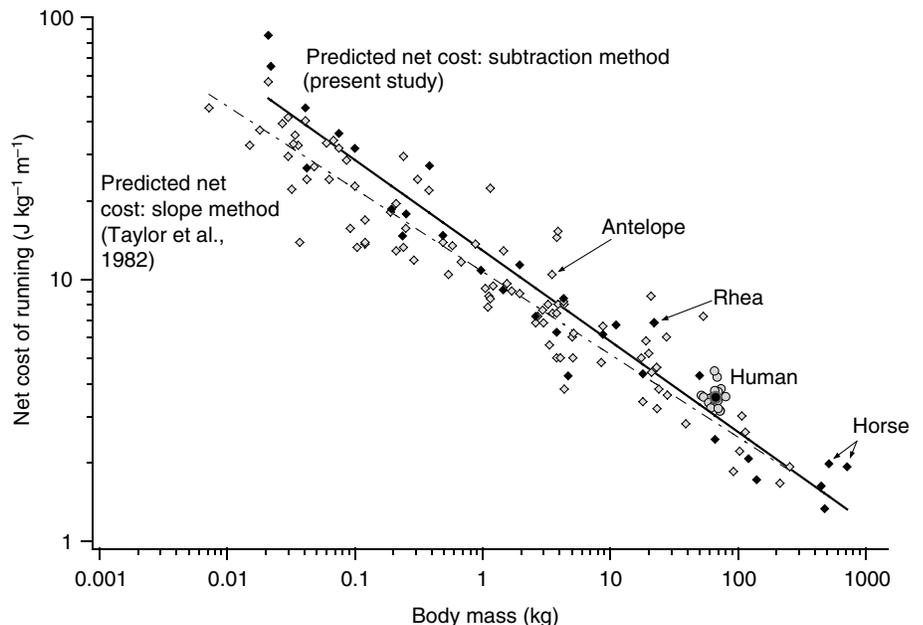
### Results

#### Comparison of human net cost of running and walking from literature

Using the slope of the regression between  $\dot{E}_{met}$  and running speed in humans (slope method) to calculate  $E_{run}$ , the mean  $E_{run}$  from 20 previously published studies was  $38 \pm 21\%$  (s.d.) above the predicted cost from the allometric equation of Taylor et al. (Taylor et al., 1982) (Eqn 1) and within the 95% confidence interval for this equation. The study with the highest cost of running was 75% above the predicted cost whereas the lowest was 2% above (Fig. 1A).

Using the gross metabolic cost minus the non-locomotor cost (subtraction method) to calculate  $E_{run}$  in humans, the mean  $E_{run}$  obtained from the published studies was  $25 \pm 11\%$  (s.d.) above

Fig. 2. Double logarithmic plot of the net energy cost of running ( $E_{run}$ ) versus body mass for humans and other mammalian and avian species. The shaded circles represent human data from 20 previously published sources (calculated from the subtraction method; see Materials and methods) (Table 1B), and the solid circle represents the mean value from these studies. The solid diamonds represent the other animals (see Table 3) used to generate the allometric equation for  $E_{run}$  using the subtraction method (Eqn 2). The solid line corresponds to the predicted  $E_{run}$  from this equation. For comparison, we have included the data points used by Taylor et al. (Taylor et al., 1982) (shaded diamonds; used to generate their allometric equation for  $E_{run}$  (Eqn 1; slope method). The broken line corresponds to the predicted  $E_{run}$  from Eqn 1.



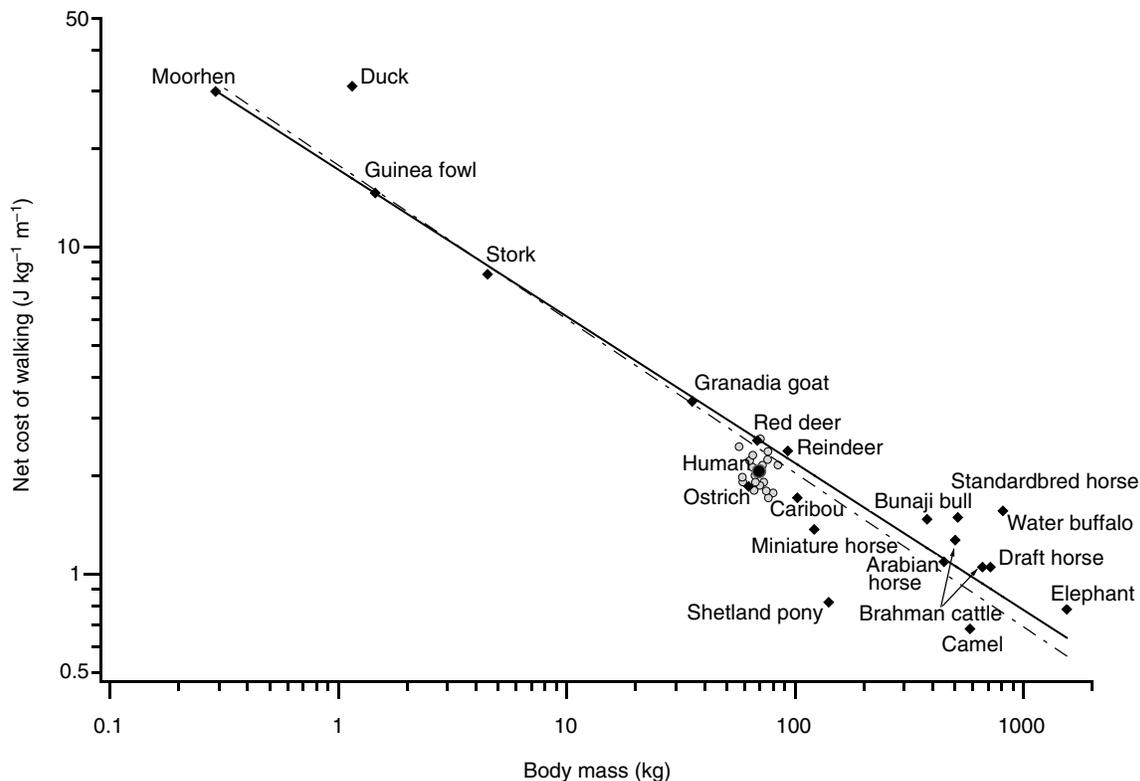


Fig. 3. Double logarithmic plot of the net energy cost of walking *versus* body mass (calculated from the subtraction method; see Materials and methods). The shaded circles represent human data from 20 previously published sources (calculated from the subtraction method, see Materials and methods) (Table 2), and the solid circle represents the mean value from these studies. The solid diamonds represent the other animals (see Table 4) used to generate the allometric equations for the net cost of walking. The solid line represents the predicted net cost of walking from the allometric equation based on animals for which either a minimum net cost of walking could be assessed or for which the net cost of walking was measured at a self-selected walking speed ( $E_{\text{walk}}$ ; Eqn 4). The broken line represents the predicted net cost of walking from the allometric equation based only on animals for which a minimum net cost of walking could be assessed ( $E_{\text{walk,min}}$ ; Eqn 3).

the predicted cost using the allometric equation of Taylor et al. (Taylor et al., 1982) and was within the 95% confidence interval of the equation. The study with the highest cost of running using the subtraction method was 57% above the predicted cost from Taylor et al. (Taylor et al., 1982) whereas the lowest was 11% above (Fig. 1B).

The new allometric equation predicting the net energy cost of running based on the  $E_{\text{run}}$  of 31 animals ranging in mass from 21 g to 715 kg and calculated using the subtraction method is:

$$E_{\text{run}} = 12.91 \pm 0.72 M_b^{-0.346(\pm 0.016)}, \quad (2)$$

where  $M_b$  is body mass in kg and  $E_{\text{run}}$  has the units  $\text{J kg}^{-1} \text{m}^{-1}$  (see Fig. 2). Values are means  $\pm$  s.e.m. and  $r^2=0.941$ . The mean  $E_{\text{run}}$  of humans based on the subtraction method was  $17 \pm 11\%$  (s.d.) above the predicted cost from Eqn 2 and fell within the 95% confidence interval of this equation. The human values ranged 4–47% above the predicted cost using Eqn 2 (Fig. 1B). Our statistical analysis revealed a significant main effect ( $P<0.001$ ) between the method used for calculating  $E_{\text{run}}$  (slope method,  $N=89$  vs subtraction method,  $N=31$ ). This represents a significant difference in the constant term of the allometric equations.

The allometric equation predicting minimum net cost of walking using the subtraction method and relying only on those

data for which a minimum net cost of walking can be assessed ( $N=15$ ) is:

$$E_{\text{walk,min}} = 17.80 \pm 2.98 M_b^{-0.471(\pm 0.037)}, \quad (3)$$

where  $E_{\text{walk}}$  has the units  $\text{J kg}^{-1} \text{m}^{-1}$  (see Fig. 3). Values are means  $\pm$  s.e.m. and  $r^2=0.927$ .

By including data of the net cost of walking at preferred speeds, the resulting allometric equation predicting the net energy cost of walking using the subtraction method ( $N=21$  with mass ranging from 290 g to 1524 kg) is:

$$E_{\text{walk}} = 17.25 \pm 2.81 M_b^{-0.449(\pm 0.032)}. \quad (4)$$

Values are means  $\pm$  s.e.m. and  $r^2=0.911$ . A significant main effect for gait (walking vs running) was observed ( $P<0.001$ ) when  $E_{\text{walk}}$  was compared to  $E_{\text{run}}$  using either the data from Taylor et al. (Taylor et al., 1982) (slope method) or  $E_{\text{run}}$  calculated from the 31 animals using the subtraction method ( $P<0.001$ ). The interaction effect between body mass and gait (walking vs running) was also significant ( $P<0.001$ ) using either  $E_{\text{run}}$  from Taylor et al. (Taylor et al., 1982) (slope method) or  $E_{\text{run}}$  calculated from 31 animals using the subtraction method. ( $P<0.001$ ). The tests of significance remained the same when  $E_{\text{walk,min}}$  was used in place of  $E_{\text{walk}}$ .

The difference between the mean human  $E_{\text{walk}}$  obtained from

Table 4. Data from the literature used to construct the allometric equations (Eqn 3 and 4) for the net energy cost of walking

Animal	Mass (kg)	$E_{\text{walk}}$ (net) (J kg <sup>-1</sup> m <sup>-1</sup> )	Non-locomotor		Speed (m s <sup>-1</sup> )	Reference
			(standing) cost (W kg <sup>-1</sup> )	Minimum examined		
<b>Mammals</b>						
Granadina goat	35.4	3.37	1.93	Yes	0.17	(Lachica et al., 1997)
Red deer	68.3	2.56	2.07	Self-selected	1.67	(Brockway and Gessaman, 1977)
Human	69.5	2.06	1.50	Yes	1.20	Mean data (see Table 2)
Reindeer	92.8	2.38	1.92	Self-selected	0.83	(White and Yousef, 1978)
Caribou	102.1	1.71	—*	Yes	1.00	(Fancy and White, 1987)
Shetland pony	140	0.82	1.35	Yes	0.64	(Hoyt and Taylor, 1981), D. F. Hoyt (personal communication)
Miniature horse	121	1.37	1.34	Yes	0.9	(Griffin et al., 2004), T. M. Griffin (personal communication)
Bunaji bulls	378	1.47	—*	Self-selected	0.97	(Dijkman and Lawrence, 1997)
Arabian horse	448	1.08	1.29	Yes	1.05	(Griffin et al., 2004), T. M. Griffin (personal communication)
Brahman cattle	501.3	1.27	—*	Self-selected	1.23	(Dijkman and Lawrence, 1997)
Standardbred horse	515.0	1.49	0.65	Yes	1.20	(Minetti et al., 1999)
Camel	582.5	0.68	0.63	Self-selected	1.12	(Yousef et al., 1989)
Brahman × Friesen cattle	660	1.05	—*	Self-selected	1.06	(Dijkman and Lawrence, 1997)
Draft horse	715	1.05	1.38	Yes	1.55	(Griffin et al., 2004), T. M. Griffin (personal communication)
Water buffalo	811.3	1.56	—*	Self-selected	1.01	(Dijkman and Lawrence, 1997)
Elephant	1542	0.78	0.92	Yes	1.00	(Langman et al., 1995)
<b>Birds</b>						
Moorhen	0.29	29.89	5.67	Yes	0.33	J. A. Carr and R. L. Marsh (personal communication)
Duck	1.15	31.03	6.67	Yes	0.33	J. A. Carr and R. L. Marsh (personal communication)
Guinea fowl	1.45	14.63	6.37	Yes <sup>†</sup>	0.50	(Marsh et al., 2004; Marsh et al., 2006), T. J. McPherson and R. L. Marsh (personal communication)
Marabou stork	4.50	8.26	3.81	Yes <sup>‡</sup>	1.02	(Bamford and Maloiy, 1980)
Ostrich	66.1	1.85	1.8	Yes	0.97	(Rubenson et al., 2004)

Net costs of walking are either from studies where a minimum cost could be assessed or from studies examining self-selected speeds and are calculated using the subtraction method (see Materials and methods).

\*Standing cost was not reported in these studies but was used by the authors (Fancy and White, 1987; Dijkman and Lawrence, 1997) to compute  $E_{\text{walk}}$ .

<sup>†</sup>Preliminary data from guinea fowl indicate that the minimum  $E_{\text{walk}}$  is not statistically different from that observed at 0.5 m s<sup>-1</sup> (T. J. McPherson and R. L. Marsh, personal communication).

<sup>‡</sup>The metabolic data (fig. 2 in Bamford and Maloiy, 1980) was scanned, digitized and fit with a 2nd order polynomial ( $y=1.20x^2-0.65x+1.29$ ;  $y$  is in ml O<sub>2</sub> s<sup>-1</sup>,  $x$  is in m s<sup>-1</sup>). This equation fitted the data better than a linear relationship, as indicated by the higher  $r$  (0.85 vs 0.65). A minimum  $E_{\text{walk}}$  is evident at ~1 m s<sup>-1</sup>.

20 previously published studies and the net energy cost of walking predicted using Eqn 3 and Eqn 4 were -15±10% and -20±9% (s.d.), respectively, and fell within the 95% confidence interval for these equations. The data used for establishing the allometric equation for  $E_{\text{walk}}$  and  $E_{\text{walk,min}}$  are presented in Table 4 and shown in Fig. 3.

### Discussion

This study re-explores how the net metabolic energy cost of human running and walking compares to those of animals of similar mass. From an extensive comparison of published human data and the adoption of a more appropriate approach to compare the net energy cost of locomotion of humans with other animal species, this study shows that the difference between the net

energy cost of human running and that predicted for an animal of similar mass is much smaller (17%) than previously estimated (~43–100%). The relative difference between humans'  $E_{\text{run}}$  and their allometrically predicted cost is comparable to or less than those of many other species, some of which are regarded as economical runners. This study also indicates that humans' net cost of walking is 20% lower than predicted for their mass. Nevertheless, this difference is not atypical given that 25% of the species examined here have a similar or lower relative cost of walking compared to that predicted for their mass.

#### Comparative cost of human running

It is difficult to establish definitively when the  $E_{\text{run}}$  of an animal should be regarded as atypical for its mass and, to the

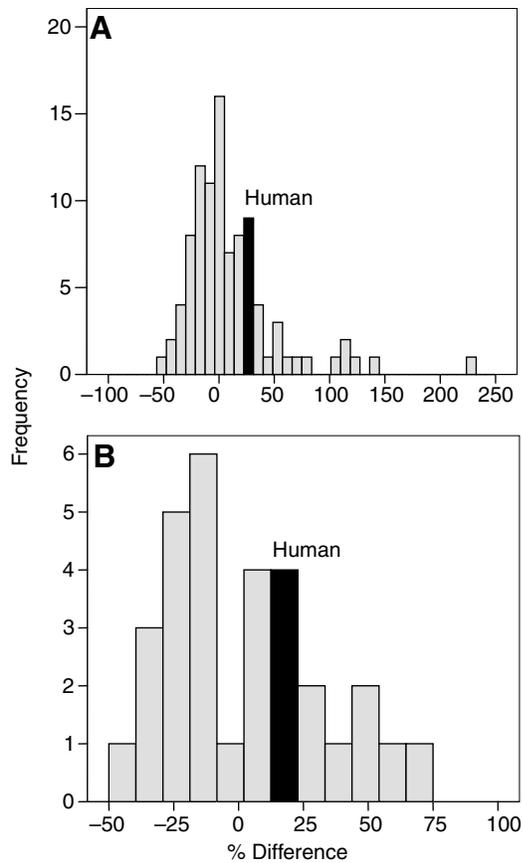


Fig. 4. Histogram of the percentage difference between the measured and allometrically predicted net cost of running ( $E_{\text{run}}$ ) using (A) the animal data from Taylor et al. (Taylor et al., 1982) ( $N=95$ ) and the allometric equation (Eqn 1) developed in their study (where  $E_{\text{run}}$  is computed using the slope method; see Materials and methods) and (B) 31 animals for which  $E_{\text{run}}$  was computed using the subtraction method and the allometric equation developed from these data (Eqn 2). The position of the mean human  $E_{\text{run}}$  based on the subtraction method from 20 previously published studies is represented by the black bars.

best of our knowledge, there is no golden standard upon which to make such a decision. Our allometric analysis nevertheless reveals that the 17% higher than predicted cost of human running is unremarkable and, in comparison with previous studies, does not warrant the labelling of humans as particularly uneconomical runners. One simple approach to gauge the cost of human running is to compare the relative difference between their measured and allometrically predicted  $E_{\text{run}}$  to those observed in other species. With respect to the allometric equation of Taylor et al. (Eqn 1), 22% of the animals used to generate this equation have an equal or greater relative difference between their measured and predicted  $E_{\text{run}}$  compared to humans (Figs 2, 4). With our new allometric equation for  $E_{\text{run}}$  using the subtraction method, 27% of the animals examined have an equal or greater relative difference between their measured and predicted  $E_{\text{run}}$  compared to humans (Figs 2, 4). Interestingly, among the animal species that have a greater relative difference between their measured and allometrically predicted  $E_{\text{run}}$  compared to humans there are several 'athletic' cursorial runners, including horses and antelope. It is also worth

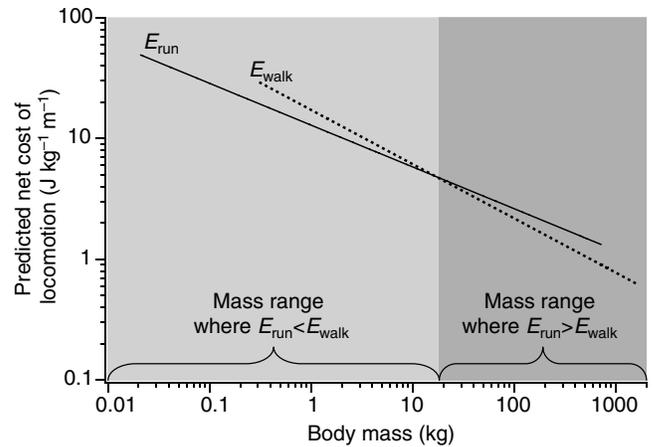


Fig. 5. The predicted net cost of running ( $E_{\text{run}}$ ) and walking ( $E_{\text{walk}}$ ) using the new allometric equation of the net cost of running (Eqn 2; solid line) and the new allometric equation of the net cost of walking (Eqn 4; broken line). The point where these relationships intersect ( $\sim 20$  kg) represents the theoretical mass where the net cost of walking and running are equivalent. Above this mass, the net cost of walking is predicted to be greater than the net cost of running, and below this mass the opposite is predicted.

considering that the 17% higher than predicted cost of  $E_{\text{run}}$  reported here in humans is not only much smaller than previously reported in the literature (43–100%) (Taylor et al., 1970; Taylor et al., 1982; Taylor, 1994) but also modest relative to the 20–27% inter-individual variation in the cost of human running (Daniels, 1985) and more than one order of magnitude smaller than the sixfold interspecies variation in the net cost of locomotion that has been reported by Full et al. (Full et al., 1990) to exist at any given body mass. Overall, given our findings and assuming that the animal species used in our allometric analysis are representative, it would be difficult to uphold that humans have an atypically high  $E_{\text{run}}$ .

The smaller differences found here between the measured and predicted  $E_{\text{run}}$  for humans compared to previously reported values is best explained on the basis of the following factors. Firstly, the higher than predicted  $E_{\text{run}}$  values for humans in the work of Taylor and colleagues (Taylor et al., 1970; Taylor et al., 1982) stems in part from the much smaller sample of human data selected for their allometric analyses. In particular, the human  $E_{\text{run}}$  values used in these analyses are among the higher values published for humans. However, it must be stressed in defence of Taylor and colleagues (Taylor et al., 1970; Taylor et al., 1982) that the purpose of their studies was not to specifically compare human  $E_{\text{run}}$  with other species but to perform an allometric analysis of  $E_{\text{run}}$  across species. Even the selection of non-representative human data would be expected to have a negligible effect on the overall scaling relationship based on a large animal sample. Secondly, another factor contributing to the higher  $E_{\text{run}}$  in humans in the allometric analyses of Taylor and colleagues is the approach adopted to calculate  $E_{\text{run}}$ . As mentioned earlier,  $E_{\text{run}}$  in allometry studies is generally estimated from the slope of the linear regression between the rate of energy expenditure and speed. This method has the advantage that it provides a single value for  $E_{\text{run}}$  that is independent of speed, a benefit that has

proven very useful for establishing general allometric scaling relationships between a large number of species moving at very different speeds. Here, we show that the use of the slope method provides a mean  $E_{\text{run}}$  that is 38% above predicted  $E_{\text{run}}$  in humans, a value similar to the 43% difference reported by Taylor et al. (Taylor et al., 1982). However, with the subtraction method to evaluate  $E_{\text{run}}$  in humans, the combined mean  $E_{\text{run}}$  from 20 previous studies falls only 25% above that predicted from the allometric equation of Taylor and colleagues (Taylor et al., 1982) and 17% above our new  $E_{\text{run}}$  allometric equation based on the subtraction method.

The larger difference between predicted and measured human  $E_{\text{run}}$  determined using the slope method compared to the subtraction method is primarily due to the marked differences between the  $y$ -intercepts of the regression equations and actual non-locomotor rates of energy expenditure. Interestingly, out of those human studies that we examined (Table 1A,B), the majority reporting steep slopes of  $\dot{E}_{\text{met}}$  vs speed (high net energy costs of running) were found to have intercepts much lower than non-locomotor metabolic rates, with some of those studies reporting negative intercepts that do not correspond to any resting physiological state (e.g. Sheppard et al., 1969; Bransford and Howley, 1977; Saunders et al., 2004b), thus resulting in an overestimation of  $E_{\text{run}}$ . Conversely, those studies reporting shallow slopes of  $\dot{E}_{\text{met}}$  vs speed (low net energy costs of running) generally have intercepts greater than non-locomotor metabolic rates. The mismatch between  $y$ -intercepts and non-locomotor metabolic rates explains, in part, the observation that there is a 70% difference in human  $E_{\text{run}}$  across studies using the slope method, with values as low as 2% above those predicted from allometry to values as high as 75% above the allometric prediction (Fig. 1A). This variability is far greater than the upper limit of 20–27% inter-individual difference in running economy in humans (Daniels, 1985). By contrast, the variability in  $E_{\text{run}}$  in humans is reduced when using the subtraction method (Fig. 1B). These findings are not surprising because the relationship between  $\dot{E}_{\text{met}}$  and speed is not linear through walking speeds in humans, with intercepts from running data in the literature (Table 1A,B) fluctuating by as much as 150%.

It is important to point out that the errors in determining  $E_{\text{run}}$  resulting from the disparity between the  $y$ -intercept and actual non-locomotor metabolic rates also affect the calculation of the net cost of running in other animal species. Perhaps the most explicit example of the unsuitability of using the slope method is the case of hopping kangaroos, where a negative slope of the linear regression between the rate of energy expenditure and speed has been reported (Dawson and Taylor, 1973). It is interesting to note that these errors have a small but statistically significant effect on the scaling relationship between  $E_{\text{run}}$  and body mass, with the slope method resulting in a lower  $E_{\text{run}}$  compared to the subtraction method (Eqn 2). This difference could be explained on the basis of a general overestimate of the non-locomotor metabolic rate using the  $y$ -intercept of the regression between metabolic rate and speed. The general scaling relationship for  $E_{\text{run}}$  (the scaling exponent) is, however, not different when using the two methods. This absence of difference is possibly because the error between the  $y$ -intercept and the actual non-locomotor cost in many animals is a small fraction of the gross metabolic rate during running and may be relatively

consistent across body mass. Therefore, since only a small difference exists between the allometric equations for  $E_{\text{run}}$  based on the subtraction and slope methods, the use of the slope method appears to be appropriate for general scaling analyses of  $E_{\text{run}}$ .

#### Comparative cost of human walking

Unlike running, the  $E_{\text{walk}}$  for humans falls moderately below the predicted values for their body mass using our new allometric analysis of  $E_{\text{walk}}$ . The lower than predicted  $E_{\text{walk}}$  in humans is also not atypical compared to the other species examined here, given that a quarter of these animals have a relatively lower  $E_{\text{walk}}$  compared to their allometrically predicted value. Also, the  $E_{\text{walk}}$  of humans is comparable to those of animals that share a similar mass, such as ostriches, caribou and deer. That there is little difference between  $E_{\text{walk}}$  in humans and these animals is somewhat surprising given that they do not possess a graviportal (straight) limb posture. Other factors that can reduce the metabolic cost of walking may balance any disadvantage that a more bent joint posture imposes on walking animals.

An unexpected and interesting finding arising from our allometric analyses is the marked significant ( $P < 0.001$ ) interaction effect between body mass and gait (walking vs running) on the net energy cost of locomotion. This interaction effect is reflected by the different exponents of the allometric relationship of the net energy cost of running [−0.316 (Taylor et al., 1982); −0.336 (present study)] and walking (−0.449) and highlights for the first time the importance of using a walk-specific allometric equation to predict the net energy costs of walking. More importantly, these results also indicate that the relative differences between  $E_{\text{walk}}$  and  $E_{\text{run}}$  in animals vary across body mass. According to our walking allometric analysis, the net energy cost of walking should be lower than that of running for large animals, but the converse for small animals (Fig. 5), and at a mass of ~20 kg, where the walking and running regression lines intersect, an animal's  $E_{\text{walk}}$  and  $E_{\text{run}}$  should in theory be equivalent. In support of this view, large animal species have an  $E_{\text{walk}}$  considerably lower than their  $E_{\text{run}}$ , as found in humans (Margaria, 1976), Shetland ponies (Hoyt and Taylor, 1981) (D. F. Hoyt, personal communication), Arabian, Draft and Miniature horses (Griffin et al., 2004) (T. M. Griffin, personal communication), Standardbred horses (Minetti et al., 1999), ostriches (Rubenson et al., 2004) and camels (Yousef et al., 1989; Evans et al., 1994) (see Tables 3 and 4) despite the gross energy cost of walking and running in several of these species being the same (Hoyt and Taylor, 1981; Griffin et al., 2004). By contrast,  $E_{\text{walk}}$  is higher compared to  $E_{\text{run}}$  in all but two of the 13 small mammal and bird species (0.021–22 kg) studied by Taylor et al. (Taylor et al., 1970) and Fedak et al. (Fedak et al., 1974). Ground squirrels (0.23 kg) (Hoyt and Kenagy, 1988) and mink (~1 kg) (Williams, 1983) also expend more energy to travel a given distance when walking compared to running. Unfortunately, the mechanisms underlying our observation that the relative differences between  $E_{\text{walk}}$  and  $E_{\text{run}}$  in animals vary across body mass remain unclear, although differences in the effectiveness of pendular and elastic energy saving strategies between large and small animals are a possible candidate (Cavagna et al., 1977). Clearly, the finding that large animals are expected to have lower walking than running net locomotor cost, and *vice versa* for small

animals, requires further corroboration and raises the question of whether this can explain some of the differences in locomotor behaviour between large and small animals.

It must be stressed that a number of precautions were taken to construct our new allometric scaling relationship for the net energy cost of walking. First, because non-locomotor rates of energy expenditure account for a greater percentage of gross metabolic rates during walking compared to running, we have used only those studies where an experimental standing non-locomotor value is provided. A second potential confounding factor relates to the fact that  $E_{\text{walk}}$  is not constant across speed for all animals. For this reason, we have computed the allometric equation for the net energy cost of walking using either only those studies where a net minimum cost of walking can be assessed ( $E_{\text{walk,min}}$ ;  $N=15$ ) or including also those studies reporting values at self-selected speeds ( $E_{\text{walk}}$ ;  $N=21$ ), as these are believed to correspond to the animals' minimum net cost of walking (Hoyt and Taylor, 1981). Our results show that both approaches yield similar findings. Given our low sample size, we also performed further analyses to determine how sensitive our allometric analysis is to the removal of data obtained from animals with either a dissimilar gait pattern (duck with their waddling gait) or leg length (stork). We found that the removal of the duck or stork from our data set did not affect significantly the scaling relationship between the net cost of walking and body mass for either  $E_{\text{walk}}$  or  $E_{\text{walk,min}}$ . Nevertheless, it is important to stress that since there are only a few studies providing data for non-locomotor and gross costs from which a minimum net cost of walking can be assessed, the scaling relationship between  $E_{\text{walk}}$  and body mass determined here suffers from the limitation that it is based on a small number of animal species. Clearly, such an allometric analysis would benefit from the inclusion of many more species.

In conclusion, by performing an extensive allometric analysis using data from the literature, we conclude that human net costs of running and walking relative to those predicted on the basis of their body mass are unremarkable compared to those of other species. For this reason, it is recommended that earlier interpretations based on the viewpoint that human locomotion is energetically atypical should be reconsidered.

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