RESEARCH ARTICLE

Minimum cost of transport in Asian elephants: do we really need a bigger elephant?

Vaughan A. Langman[1,*], Michael F. Rowe[2], Thomas J. Roberts[3], Nathanial V. Langman[4] and
Charles R. Taylor[5]

[1]USDA/APHIS, 816 White Pine Drive, Bellvue, CO 80512, USA, [2]Biology Department, Indiana State University, Terre Haute,
IN 47802, USA, [3]Ecology and Evolutionary Biology, Brown University, Providence, RI 02912, USA, [4]Thayer School of Engineering,
Dartmouth College, Hanover, NH 03755, USA and [5]Concord Field Station, Harvard University, Bedford, MA 01730, USA

*Author for correspondence (vaughan.a.langman@aphis.usda.gov)

SUMMARY

Body mass is the primary determinant of an animal's energy requirements. At their optimum walking speed, large animals have lower mass-specific energy requirements for locomotion than small ones. In animals ranging in size from 0.8g (roach) to 260kg (zebu steer), the minimum cost of transport (COT_{min}) decreases with increasing body size roughly as $COT_{min} \propto$ body mass $(M_b)^{-0.316 \pm 0.023}$ (95% CI). Typically, the variation of COT_{min} with body mass is weaker at the intraspecific level as a result of physiological and geometric similarity within closely related species. The interspecific relationship estimates that an adult elephant, with twice the body mass of a mid-sized elephant, should be able to move its body approximately 23% cheaper than the smaller elephant. We sought to determine whether adult Asian and sub-adult African elephants follow a single quasi-intraspecific relationship, and extend the interspecific relationship between COT_{min} and body mass to 12-fold larger animals. Physiological and possibly geometric similarity between adult Asian elephants and sub-adult African elephants caused body mass to have a no effect on COT_{min} ($COT_{min} \propto M_b^{0.007 \pm 0.455}$). The COT_{min} in elephants occurred at walking speeds between 1.3 and ~1.5ms⁻¹, and at Froude numbers between 0.10 and 0.24. The addition of adult Asian elephants to the interspecific relationship resulted in $COT_{min} \propto M_b^{-0.277 \pm 0.046}$. The quasi-intraspecific relationship between body mass and COT_{min} among elephants caused the interspecific relationship to underestimate COT_{min} in larger elephants.

Key words: Asian elephant, locomotion, cost of transport, allometry.

INTRODUCTION

Body mass is the primary determining factor of an animal's total energy requirements (Calder, 1984; Schmidt-Nielsen, 1984; West and Brown, 2005; McNab, 2008). Large animals use less energy per kilogram body mass for locomotion than small animals. African (*Loxodonta africana*) and Asian elephants (*Elephas maximus*) represent the upper limit of body mass in extant terrestrial mammals, and large bulls can weigh up to 7500kg (Nowak, 1999). Although physiological measurements on elephants are technically challenging, experiments using well-trained captive elephants allow modeling of the biomechanical and energetic characteristics of locomotion in the largest terrestrial mammals (Alexander et al., 1979; Langman et al., 1995; Hutchinson et al., 2003; Hutchinson et al., 2006; Ren and Hutchinson, 2008; Ren et al., 2010; Genin et al., 2010).

The mass-specific total cost of transport (COT_{tot}; $Jkg^{-1}m^{-1}$) is the amount of energy required to move 1kg of body mass over 1m. Animals, including elephants, prefer to walk at a speed near the mid-range within a walking gait, where COT_{tot} is minimized (Pennycuik, 1975; Hoyt and Taylor, 1981; Taylor et al., 1982; Alexander, 1989; Full and Tu, 1991; Griffin et al., 2004; Rubenson et al., 2007; Maloiy et al., 2009). Because the minimum total cost of transport (COT_{min}) provides a biologically meaningful parameter for comparison, Taylor et al. (Taylor et al., 1982) used data from approximately 90 species of mammals ranging in size from 7g (pygmy mouse) to 260kg (zebu steer) to develop an interspecific

allometric equation that describes the decrease in COT_{min} with increased body mass:

$$COT_{min} = 10.7 \pm 0.663 M_b^{-0.316 \pm 0.023}, \qquad (1)$$

where M_b is body mass (kg) [values shown are presented ±95% confidence intervals (CIs)]. To extend the range of data towards the lower limits of body mass, Full and Tu (Full and Tu, 1991) added reptiles, crustaceans, myriapods and insects with body mass as low as 0.8g and obtained approximately the same equation as that reported by Taylor et al. (Taylor et al., 1982), $COT_{min}=10.8M_b^{-0.32}$. To extend the range of data towards the upper limits of body mass, Langman et al. (Langman et al., 1995) added sub-adult African elephants, with an average body mass six times that of the largest animal used in Taylor et al. (Taylor et al., 1982). The COT_{min} of young African elephants were within the 95% CIs of Eqn 1. The application of Eqn 1 to adult Asian elephants, twice the size of the elephants reported by Langman et al. (Langman et al., 1995), estimates that COT_{min} in larger elephants should be reduced by approximately 23% when compared with COT_{min} in sub-adult African elephants.

An analysis of intraspecific variability is complementary to interspecific analyses (Bennett, 1987). Because of geometric and physiological similarity, body mass does not have the same effect on COT_{min} at the intraspecific level, or between closely related species, as it does at the interspecific level. In geometrically similar

species, juveniles have the same relative dimensions as adults, just on a smaller scale. As a result, muscle and skeletal morphology of small and large individuals are similar. Both equines and camels show intraspecific geometric similarity. The slope of the intraspecific relationship between COT_{min} and body mass is nearly flat ($\approx M_b^0$) in both horses from 90 to 720 kg (Griffin et al., 2004) and camels from 240 to 580 kg (Yousef et al., 1989; Maloiy et al., 2009) compared with the interspecific relationship $M_b^{-0.316}$ (Eqn 1). African and Asian elephants, along with extinct mammoths (*Mammuthus*), comprise the family Elephantidae and share common ancestry (Haynes, 1991; Krause et al., 2006). All elephants are graviportal species, i.e. species with column-like limbs and a bone structure that distributes their enormous body mass across a sizeable foot surface (Gray, 1968; Coombs, 1978; Yates and Kitching, 2003). However, subtle differences in limb geometry exist between African and Asian elephants (Kokshenev and Christiansen, 2010). Sub-adult African and adult Asian elephants might be geometrically similar enough that they follow a quasi-intraspecific relationship, where the decrease in COT_{min} with increasing body mass is less than $M_b^{-0.316}$.

In this study, we first test the hypothesis that adult Asian elephants and sub-adult African elephants are physiologically similar and geometrically similar enough, as reported in horses and camels, that larger body mass will not bring about a reduction in COT_{min}. If elephants within a 2.5-fold range of body mass are physiologically and geometrically similar, then the slope of COT_{min} *versus* body mass will approach M_b^0. Second, we discuss the effect that the addition of elephants, with 12 times the body mass of the largest animal used by Taylor et al. (Taylor et al., 1982), has on the interspecific relationship between COT_{min} and body mass. If the intraspecific relationship applies to elephants, then COT_{min} measured in increasingly larger elephants will show sequentially greater deviation away from COT_{min} estimated using the interspecific relationship of $M_b^{-0.316}$. Therefore, we have measured the COT_{min} in adult Asian elephants and combined these results with those for smaller African elephants reported by Langman et al. (Langman et al., 1995).

MATERIALS AND METHODS
Elephants
Two adult female Asian elephants *Elephas maximus* Linnaeus 1758 (Panya and Jean; Table 1) housed at the Audubon Zoo in New Orleans, LA, USA, were used for all of the metabolic measurements. Both elephants were very tractable and well trained by their keepers. Their feeding schedule was unaltered and water was available *ad libitum* except during the exercise trials. All methods were approved by the Audubon Zoo Institutional Animal Care and Use Committee.

Experimental procedure
Oxygen consumption was measured using the techniques reported by Langman et al. (Langman et al., 1995) to quantify metabolic rates at rest and during exercise from African elephants. The elephants were trained, for 1 week prior to measurements, to wear

Fig. 1. Open-system measurement of resting oxygen consumption in a female Asian elephant prior to exercise at Audubon Zoo, New Orleans, LA, USA.

a loose-fitting mask that enclosed both the trunk and mouth for open-system oxygen consumption measurements. The elephants were fitted with the mask, and metabolic measurements then made while the elephants stood quietly or walked up to three laps around the level 0.5 km oval track in the interior of the zoo (Fig. 1). The mask was connected to a 1 hp industrial blower (Dayton, Niles, IL, USA) mounted on a motorized golf cart that was fitted with a bicycle wheel equipped with a calibrated electronic speedometer to record speed. The blower was previously calibrated in laboratory conditions to meter air flow through the mask at a rate of 108 l s^{-1}, a flow rate that ensured the elephants' exhaled air was drawn through the mask. The elephants walked the first lap at a slow pace and sequentially increased speed on the following laps. A small sample of the air flow exiting the mask was collected in a 200 l Douglas bag (Harvard Apparatus, Holliston, MA, USA) over a 5 min period in the later stages of walks. The sample was analyzed for oxygen concentration with a paramagnetic oxygen analyzer (Taylor Servomex OA272, Woburn, MA, USA). The entire system was calibrated by metering nitrogen into the mask (Fedak et al., 1981) and the accuracy was better than ±2%.

Data analyses
Mass-specific total energy expenditure (EE_{tot}; W kg^{-1}) is the amount of energy expended per kilogram body mass for both the postural cost of standing, i.e. standing metabolic rate, and the energy expended to move the body's center of mass both horizontally and vertically during locomotion (Schmidt-Nielsen, 1972). The EE_{tot} in the elephants was calculated from the rate of oxygen consumption recorded during exercise and applying an energetic equivalent of 20.1 J to 1 ml O_2 consumed.

Mass-specific net energy expenditure (EE_{net}) is the amount of energy required for locomotion above that required for the postural cost of standing (Schmidt-Nielsen, 1972). The EE_{net} was calculated by subtracting resting energy expenditure (Table 1) from EE_{tot}

Table 1. Characteristics and mean (±s.d.) resting mass-specific energy expenditure in two Asian elephants

Elephant	Age (yr)	Mass (kg)	Energy expenditure (W kg^{-1})	Trials
Panya	31	3545	0.74±0.11	10
Jean	23	2682	0.77±0.11	10

Note: these measurements were similar to a resting energy expenditure of 0.60 W kg^{-1} in a female Asian elephant (3672 kg) reported by Benedict (Benedict, 1936).

Table 2. Minimum mass-specific total cost of transport (COT$_{min}$) recorded in elephants, the Froude number (Fr) at which COT$_{min}$ occurred, second-order polynomial equations and estimated COT$_{min}$ in three African and two Asian elephants

Genus	Elephant	Mass (kg)	Hip height (m)	Recorded COT$_{min}$ (J kg^{-1} m^{-1})	Fr	Polynomial equation	Estimated COT$_{min}$ (J.kg^{-1} m^{-1})	R^2	Trials
Loxodonta	Kelly	1435	1.52	1.35[a]	0.11	16.7Fr^2–6.96Fr+2.27	1.54	0.56	12
	Tara	1525	1.55	1.19[a]	0.12	84.7Fr^2–25.8Fr+3.18	1.21	0.98	5
	Dottie	1667	1.53	1.62	0.14	86.0Fr^2–17.5Fr+2.51	1.62	1	3
Elephas	Jean	2682	1.68	1.34	0.09	181.6Fr^2–56.1Fr+5.36	1.03	0.58	15
	Panya	3545	1.83	1.11	0.08	112.5Fr^2–37.1Fr+3.94	0.88	0.60	24

[a]These measurements were within the 95% confidence intervals of Eqn 1 (see the Introduction) reported by Taylor et al. (Taylor et al., 1982).

Table 3. Range of Froude numbers (Fr), and mean (±s.d.) walking speed, mass-specific minimum cost of transport (COT$_{min}$), and whole-animal COT$_{min}$ recorded in three African and two Asian elephants

Genus	Elephant	Mass (kg)	Fr	Speed (m s^{-1})	COT$_{min}$ (J kg^{-1} m^{-1})	Whole-animal COT$_{min}$ (J m^{-1})	Trials
Loxodonta	Kelly	1435	0.11–0.24	1.5±0.2	1.54±0.13	2210±187	5
	Tara	1525	0.12–0.19	1.5±0.2	1.33±0.17	2029±260	3
	Dottie	1667	0.10–0.14	1.4±0.1	1.69±0.09	2817±150	2
Elephas	Jean	2682	0.10–0.17	1.5±0.2	1.66±0.22	4452±590	7
	Panya	3545	0.10–0.17	1.5±0.2	1.42±0.15	5034±532	9

recorded during exercise. It was not always possible to make resting measurements prior to each exercise trial or make an equal number of trials at each walking speed. Therefore, the mean resting energy expenditure recorded for individual elephants was used to calculate EE$_{net}$.

Mass-specific COT$_{tot}$ was calculated by dividing the EE$_{tot}$ measured during exercise by the speed of locomotion (m s^{-1}). The net cost of transport (COT$_{net}$) estimates the amount of energy required to move 1 kg of body mass over 1 m during locomotion above that required for standing quietly (Schmidt-Nielsen, 1972). COT$_{net}$ was calculated by subtracting the average resting energy expenditure of individual elephants from EE$_{tot}$ prior to dividing by the speed of locomotion.

Energetic similarity between adult Asian and sub-adult African elephants was determined by plotting COT$_{tot}$ *versus* Froude number:

$$Fr = v_f^2 / (g \times h_{hip}), \qquad (2)$$

a dimensionless measure of speed calculated by dividing the squared forward velocity of locomotion (v_f; m s^{-1}) by gravitational acceleration (g; 9.8 m s^{-2}) and hip height (h_{hip}; m) (Alexander and Jayes, 1983). The COT$_{min}$ for individual elephants was estimated from second-order polynomial equations that describe the relationship between COT$_{tot}$ and Froude number. The estimated COT$_{min}$ was compared with minimum recorded COT$_{min}$ (Table 2). However, because there was no clearly distinguishable COT$_{min}$ in adult Asian elephant, we calculated the mean (±s.d.) COT$_{min}$ by averaging the COT$_{tot}$ measured over the range of Froude numbers that minimized cost in individual elephants (Table 3). The calculated mean COT$_{min}$ was used to develop intraspecific and interspecific allometric relationships between COT$_{min}$ and body mass.

Studies of animal energetics are usually conducted by subjecting animals to evenly spaced increases in treadmill speed (Hoyt and Taylor, 1981; Taylor et al., 1982; Full and Tu, 1991; Griffin et al., 2004; Rubenson et al., 2007; Maloiy et al., 2009). These conditions allow for equal sample sizes of repeated trials at each tread speed, i.e. treatment groups. However, treadmills suitable for elephants are rare, and so our data and those reported by Langman et al. (Langman et al., 1995) were obtained by walking zoo elephants on an outdoor track. The resulting small sample size and unpaired continuous data reduced the power of our statistical analyses (Sokal and Rohlf, 1995).

KaleidaGraph 4.03 (Synergy Software, Reading, PA, USA) was used for graphing and statistical analyses.

RESULTS
Energy expenditure
The results of our measurements of resting energy expenditure in Asian elephants (Table 1) were similar to those reported by Benedict (Benedict, 1936). During locomotion at speeds ranging from 0.13 to 2.2 m s^{-1}, the EE$_{tot}$ for the larger Asian elephant, Panya, generally was less than that measured for the smaller elephant, Jean (Fig. 2). At the fastest walking speed, EE$_{tot}$ increased approximately 4.5-fold over resting measurements. Over approximately the same range
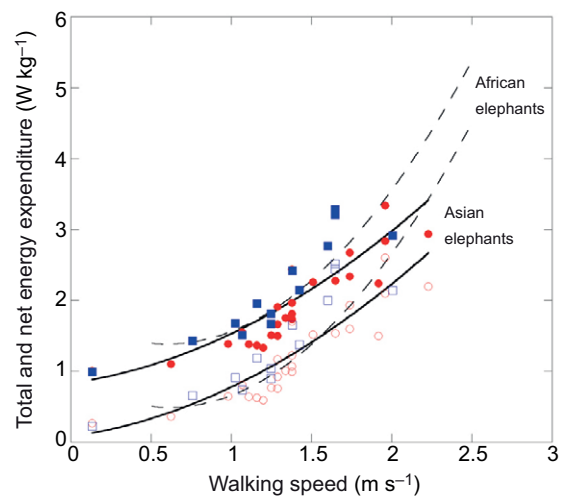

Fig. 2. Mass-specific total (solid symbols) and net energy expenditure (open symbols) (EE$_{tot}$ and EE$_{net}$; W kg^{-1}) in two adult Asian elephants (Panya, red circles; Jean, blue squares) at walking speeds ranging from 0.13 to 2.2 m s^{-1}. The equation describing the curvilinear increase in EE$_{tot}$ with walking speed is EE$_{tot}$=0.35v_f^2+0.42v_f+0.75, where v_f is walking speed (m s^{-1}) (R^2=0.88). The equation describing the curvilinear increase in EE$_{net}$ with walking speed is EE$_{net}$=0.38v_f^2+0.32v_f+0.08 (R^2=0.75). The mean EE$_{tot}$ and EE$_{net}$ in three sub-adult African elephants (dashed lines) walking at speeds ranging from 0.44 to 2.5 m s^{-1} reported by Langman et al. (Langman et al., 1995) are presented for comparison.
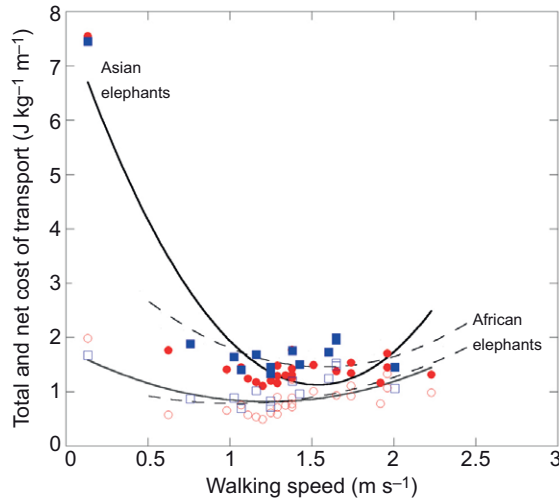
Fig. 3. Mass-specific total (solid symbols) and net cost of transport (open symbols) (COT_{tot} and COT_{net}; $J\,kg^{-1}\,m^{-1}$) in two Asian elephants (Panya, red circles; Jean, blue squares) at walking speeds from 0.13 to $2.2\,m\,s^{-1}$. The equation describing the curvilinear relationship between COT_{tot} and walking speed is $COT_{tot}=2.8v_f^2-8.7v_f+7.8$, where v_f is walking speed ($m\,s^{-1}$) (R^2=0.85). Note that the curve for Asian elephants is strongly affected by the high leverage of the data points at the exceptionally slow walking speed of $0.13\,m\,s^{-1}$, and thus the walking speed for minimum COT (COT_{min}) is not clearly defined. The equation describing the curvilinear relationship between COT_{net} and body mass is $COT_{net}=0.64v_f^2-1.6v_f+1.8$ (R^2=0.40). The mean COT_{tot} and COT_{net} in three sub-adult African elephants (dashed lines) walking at speeds ranging from 0.44 to $2.5\,m\,s^{-1}$ reported by Langman et al. (Langman et al., 1995) are presented for comparison.

Fig. 4. Second-order polynomial equations (Table 2) describing the quasi-intraspecific relationships between estimated total cost of transport (COT_{tot}) and Froude number in two adult Asian elephants (Panya, red solid line; Jean, blue solid line) and three sub-adult African elephants (Kelly, dotted line; Tara, short dashed line; Dottie, long dashed line). The estimated minimum cost of transport occurred over a narrow range of Froude numbers, from 0.1 to 2.4.

of walking speeds, from 0.4 to $2.5\,m\,s^{-1}$, the EE_{tot} in sub-adult African elephants reported by Langman et al. (Langman et al., 1995) was comparable to EE_{tot} measured in Asian elephants (Fig. 2). Similarly, EE_{net} (Fig. 2) tended to be lower in the larger elephant. At the fastest walking speed of $2.2\,m\,s^{-1}$, EE_{net} increased approximately 11-fold over the slowest walking speed of $0.13\,m\,s^{-1}$. The EE_{net} in Asian elephants was comparable to EE_{net} in sub-adult African elephants reported by Langman et al. (Langman et al., 1995).

Cost of transport

Over the range of walking speeds tested, the COT_{tot} was generally lower in the larger Asian elephant, Panya (Fig. 3). COT_{min} values, calculated from the polynomial equation describing the relationship between COT_{tot} and walking speed, in adult Asian elephants (Fig. 3) were less than recorded COT_{min}. Similarly, the larger elephant recorded lower COT_{net}. The COT_{net} recorded in Asian elephants in the present study was comparable to COT_{net} in African elephants reported by Langman et al. (Langman et al., 1995). The COT_{min} calculated from the polynomial equation describing the relationship between COT_{net} and walking speed of $0.80\,J\,kg^{-1}\,m^{-1}$ recorded in Asian elephants (Fig. 3) was similar to the COT_{min} of $0.78\,J\,kg^{-1}\,m^{-1}$ reported in African elephants (Langman et al., 1995).

DISCUSSION
Optimum walking speed in Asian elephants

Elephants in nature generally choose to walk at a slow pace and only use fast locomotion when disturbed (Moss, 1988; Douglas-Hamilton et al., 2005; Joshi, 2009). At slow walking speeds, kinematic and kinetic variables that define the walking gait in African and Asian elephants are quite similar (Hutchinson et al.,
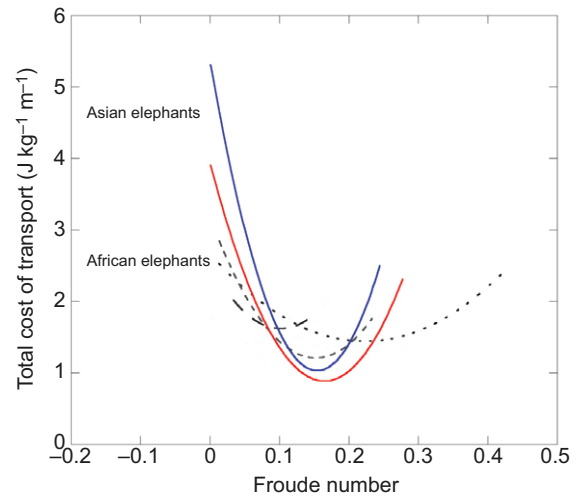
2006; Ren and Hutchinson, 2008; Genin et al., 2010). Analyses of COT_{tot} and COT_{net} using polynomial equations (Fig. 3) could not characterize optimum walking speed in Asian elephants because of the similarity in COT_{min} measurements recorded at speeds between 0.5 and $2.2\,m\,s^{-1}$. However, recorded and estimated minimum total cost of transport (Table 2, Fig. 4) occurred at speeds and Froude numbers similar to the biomechanical optimum walking speed of approximately $1.3\,m\,s^{-1}$ and a Froude number of 0.09 reported by Ren and Hutchinson (Ren and Hutchinson, 2008) and Genin et al. (Genin et al., 2010).

The minimum walking speed reported here of $0.13\,m\,s^{-1}$ was the result of the Asian elephants' willingness to walk at an extremely slow pace, in comparison to the reluctance of young African elephants to walk slower than $0.44\,m\,s^{-1}$ (Langman et al., 1995). Therefore, the large difference in COT_{tot} between slow-walking Asian and African elephants (Fig. 3) is the result of different sampling intervals and not physiological differences between species. The maximum walking speed of Asian and African elephants, 2.2 and $2.5\,m\,s^{-1}$, respectively, was limited by the maximum speed of the golf cart when heavily loaded with respirometry equipment (Fig. 1), not by the ability of the elephants to walk faster.

Indeed, elephants are capable of fast locomotion; they have a maximum recorded walking speed of $6.8\,m\,s^{-1}$ (Hutchinson et al., 2003). However, fast locomotion comes with a high energetic cost (Fig. 2). At fast speeds of locomotion, nearly all animals switch from the pendulum-like mechanism characteristic of the walking gait to a more elastic mechanism characteristic of a running gait (Alexander, 1991). Elephants differ somewhat from this pattern. Elephants exhibit substantial limb compliance during the walking gait (Ren et al., 2010), which defies the characterization of elephants as stiff-legged graviportal species (Gray, 1968; Coombs, 1978; Yates and Kitching, 2003). In elephants, limb compliance increases with locomotion speed, which results in increased joint flexion and dampening of ground forces on the limbs (Ren et al., 2010). However, as joint flexion increases a greater muscle volume is
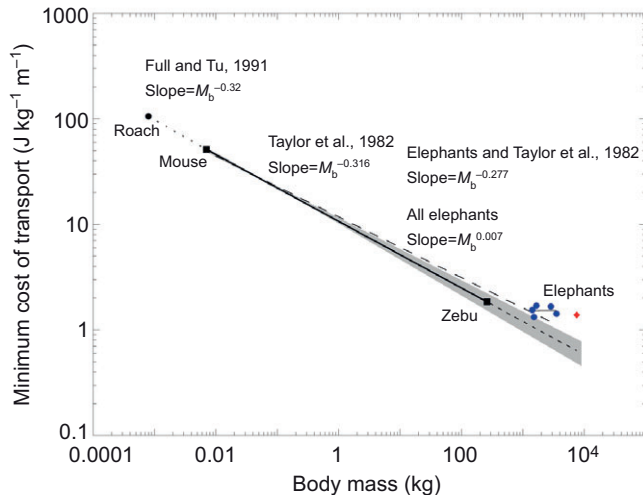
Fig. 5. Interspecific relationship between minimum cost of transport
(COT$_{min}$; J kg^{-1} m^{-1}) and body mass (M_b; kg) in terrestrial animals ranging
in size from 0.8 g to 3545 kg. The relationship between COT$_{min}$ and body
mass in reptiles, amphibians, crustaceans, myriapods and insects ranging
in size from 0.8 g to approximately 1 kg is represented by the allometric
equation COT$_{min}$=10.8$M_b^{-0.32}$ (dotted line) (Full and Tu, 1991). The
relationship between COT$_{min}$ and body mass in mammals ranging in size
from 7 g to 260 kg is represented by the allometric equation
COT$_{min}$=10.7±0.663$M_b^{-0.316±0.023}$ (95% CI) (solid line) (Taylor et al., 1982).
The addition of adult Asian elephants and sub-adult African elephants (blue
circles) to data from Taylor et al. (Taylor et al., 1982) produced the
equation COT$_{min}$=11.9±3.30$M_b^{-0.277±0.046}$ (long dashed line). The quasi-
intraspecific relationship within elephants is described by the allometric
equation COT$_{min}$=1.43±0.07$M_b^{0.007±0.455}$ (short dashed line). We estimate
the COT$_{min}$ in a large (7500 kg) elephant (red diamond) to be approximately
1.52 J kg^{-1} m^{-1}.

The recorded mean (±s.d.) COT$_{min}$ in all elephants occurred over
a narrow range of Froude numbers (Table 3, Fig. 4). The equation
describing the quasi-intraspecific relationship between COT$_{min}$ and
body mass within elephants is COT$_{min}$=1.44±0.07$M_b^{0.007±0.455}$
(R^2=0.01; Fig. 5). Within elephants, the COT$_{min}$ is not a function of
$M_b^{-0.316}$, as is characteristic of the interspecific relationship (Eqn 1)
reported by Taylor et al. (Taylor et al., 1982), but is a function of
≈M_b^0, characteristic of the intraspecific relationship reported in
horses and camels (Yousef et al., 1989; Griffin et al., 2004; Maloiy
et al., 2009).

Do we really need a bigger elephant?
Adult Asian and sub-adult African elephants are physiologically
similar and geometrically similar enough to influence the
interspecific relationship between COT$_{min}$ and body mass. The
addition of Asian elephants, with a 12-fold increase in body mass
over the largest animal used by Taylor et al. (Taylor et al., 1982),
produced an allometric relationship for mammals ranging in size
from 7 g to 3545 kg (COT$_{min}$=11.9±3.30$M_b^{-0.277±0.046}$; Fig. 5).

The mean COT$_{min}$ in two adult Asian elephants (Table 3) was
approximately the same as the mean COT$_{min}$ in three sub-adult African
elephants reported by Langman et al. (Langman et al., 1995), not
23% lower as estimated by Eqn 1. The difference between COT$_{min}$
measured in elephants and that predicted by Eqn 1 was due to the
influence of physiological similarity within elephants. The mean
COT$_{min}$ in individual elephants (Table 3) ranged from 27 to 88% above
that predicted by Eqn 1. If the intraspecific relationship is extrapolated
to even larger elephants, physiological similarity will cause greater
divergence from the Taylor et al. (Taylor et al., 1982) equation. It is
unlikely that the COT$_{min}$ in a larger elephant (with a body mass of
7500 kg) would be significantly lower than the values we report here.
Based on the slopes of the relationship between COT$_{min}$ and body
mass within elephants, i.e. $M_b^{0.007}$, and that of the interspecific
relationship, i.e. $M_b^{-0.316}$, the COT$_{min}$ of large bull elephants will be
approximately 138% above that predicted by Eqn 1.

LIST OF SYMBOLS
COT$_{min}$	Mass-specific minimum cost of transport (J kg^{-1} m^{-1})
COT$_{net}$	Mass-specific net cost of transport (J kg^{-1} m^{-1})
COT$_{tot}$	Mass-specific total cost of transport (J kg^{-1} m^{-1})
EE$_{net}$	Mass-specific net energy expenditure (W kg^{-1})
EE$_{tot}$	Mass-specific energy expenditure (W kg^{-1})
Fr	Froude number (dimensionless speed)
g	Gravitational acceleration (9.8 m s^{-2})
M_b	Body mass (kg)
v_f	Walking speed (m s^{-1})

required to support the great body mass of elephants (Ren et al.,
2010). In response, elephants may experience a linear increase in
energy expenditure at walking speeds greater than the maximum
we report in the present study. Although we acknowledge the
dangers of extrapolation, using the second-order polynomial
equation relating EE$_{tot}$ to walking speed (R^2=0.88; Fig. 2), we
estimate that it would require a 26-fold increase EE$_{tot}$ above rest
(Table 1) for the Asian elephants reported here to walk at 6.8 m s^{-1}.
The estimated increase in EE$_{tot}$ in fast-walking elephants is
comparable to near-maximum increases in energy expenditure
recorded in donkeys and camels of 22- and 32-fold, respectively
(Evans et al., 1994; Mueller et al., 1994).

Physiological similarity between adult Asian and sub-adult African elephants
African and Asian elephants ranging in body mass from 1435 to
3545 kg are physiologically similar and geometrically similar enough
that mass-specific COT$_{min}$ among individual elephants is similar
(Table 3, Fig. 4). However, it should be noted that the whole-animal
COT$_{min}$ (J m^{-1}), the ecologically relevant level of analyses, indicates
that the two larger Asian elephants would require 1.6- to 2.4-fold
more energy for locomotion than the three smaller African elephants
(Table 3). Some populations of both African and Asian elephants
engage in seasonal migrations (Guy, 1976; Sukumar, 1989;
Tchamba, 1993; Thouless, 1995; Joshi, 2009). As a result of
variations in whole-animal COT$_{tot}$ between adult and sub-adult
elephants, migration might result in differential intraspecific
energetic challenges, a topic worthy of further investigation.

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