

Phylogenetic comparisons of pedestrian locomotion costs: confirmations and new insights

Craig R. White^{1,2}, Lesley A. Alton^{1,2}, Taryn S. Crispin² & Lewis G. Halsey³

¹Centre for Geometric Biology, School of Biological Sciences, Monash University, Melbourne, Victoria 3800, Australia

²School of Biological Sciences, The University of Queensland, Brisbane, Queensland 4072, Australia

³Department of Life Sciences, Centre for Research in Ecology, University of Roehampton, Holybourne Avenue, London, SW15 4JD, UK

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Correspondence

Craig R. White, Centre for Geometric Biology, School of Biological Sciences, Monash University, Melbourne, Vic. 3800, Australia.

Tel: +61 (0) 3 9902 0769;

E-mail: craig.white@monash.edu

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Abstract

The energetic costs for animals to locomote on land influence many aspects of their ecology. Size accounts for much of the among-species variation in terrestrial transport costs, but species of similar body size can still exhibit severalfold differences in energy expenditure. We compiled measurements of the (mass-specific) minimum cost of pedestrian transport (COT_{min} , mL/kg/m) for 201 species – by far the largest sample to date – and used phylogenetically informed comparative analyses to investigate possible eco-evolutionary differences in COT_{min} between various groupings of those species. We investigated number of legs, ectothermy and endothermy, waddling, and nocturnality specifically in lizards. Thus, our study primarily revisited previous theories about variations in COT_{min} between species, testing them with much more robust analyses. Having accounted for mass, while residual COT_{min} did not differ between bipedal and other species, specifically waddling bipeds were found to have relatively high COT_{min} . Furthermore, nocturnal lizards have relatively low COT_{min} although temperature does not appear to affect COT_{min} in ectotherms. Previous studies examining across-species variation in COT_{min} from a biomechanical perspective show that the differences between waddling birds and nonwaddling species, and between nocturnal lizards and other ectotherms, are likely to be attributable to differences in ground reaction forces, posture, and effective limb length.

Introduction

Many animals spend a substantial part of their time moving around. For them, locomotion is a fundamental aspect of finding food, escaping from predators, attracting mates, dispersing, and migrating. To move themselves, animals must exert force on their surrounding environment to overcome friction and gravity, and this requires energy to be consumed via cellular work. The energetic cost of locomotion can therefore be considerable (Garland 1983; Speakman and Selman 2003; Rezende et al. 2009; Gefen 2011; Scantlebury et al. 2014; Halsey et al. 2015) and may influence an animal's fitness by constraining the amount of energy it can allocate to growth and reproduction. Consequently, understanding what influences the energetic cost of locomotion in animals has been the subject of much research.

An animal's energetic cost of locomotion can be quantified by measuring its metabolic rate (usually as rate of

oxygen consumption) while moving at a constant speed, once its cardio-respiratory physiology has reached steady state. For most, but not all, species, metabolic rate during locomotion is linearly related to speed to at least a good approximation (Taylor et al. 1970, 1982; Schmidt-Nielsen 1972b), for example, Figure 1. The slope of the linear regression relating metabolic rate and speed represents a speed-independent minimum cost of transport (COT_{min} , mL of O_2 consumed per kg of body mass per m traveled). COT_{min} estimates the energy expended over and above the y -intercept of the relationship between metabolic rate and speed, where the y -intercept estimates the energetic cost of an animal traveling at a speed of zero: the costs of body maintenance and of holding the body posture associated with movement (see Halsey 2013 for discussion of the y -intercept). Thus, COT_{min} is the theoretical minimum rate of energy expenditure possible by an animal to locomote, that is, if it were able to nullify the costs of other processes not directly related to it moving.

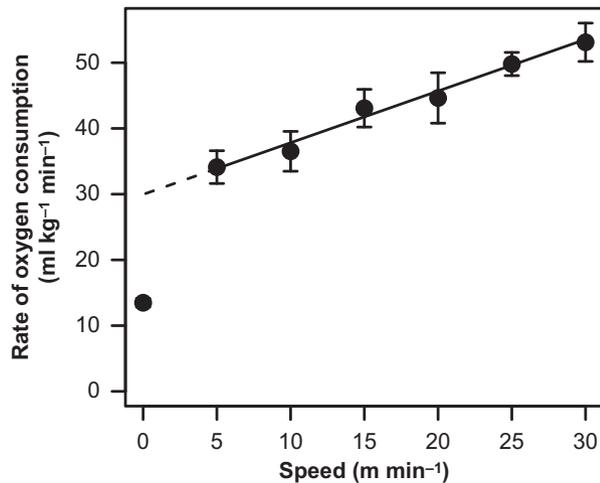


Figure 1. The relationship between rate of oxygen consumption (a proxy for metabolic rate: Lighton and Halsey 2011) and locomotion speed for cormorants *Phalacrocorax carbo* undergoing pedestrian locomotion on a treadmill (data from White et al. 2008a; see also the Supporting information associated with White et al. 2011 for an example of a raw data trace for such an experiment). Filled circles represent mean values of rate of oxygen consumption measured at rest and a range of locomotion speeds and are shown \pm SE. The solid line indicates the best fit linear relationship between rate of oxygen consumption and speed during locomotion. The slope of this line represents a speed-independent minimum cost of transport (COT_{min} , mL of O_2 consumed per kg of body mass per meter traveled), which represents the energy expended over and above the y -intercept of the relationship between metabolic rate and locomotion speed. The dashed line is extrapolated to a speed of 0 m/sec; as is often the case the extrapolated y -intercept falls above the measured resting rate of oxygen consumption (see Halsey 2013 for further discussion of the elevated y -intercept).

While COT_{min} does not account for all energy costs associated with locomotion, and its calculation assumes a perfect linear relationship between rate of oxygen consumed and locomotion speed, being independent of speed it nonetheless provides an invaluable metric by which to compare movement costs across distantly related and greatly differing animals (Halsey et al. 2016). As is the case for a wide range of physiological traits (Calder 1984; Schmidt-Nielsen 1984; White and Kearney 2014), a considerable proportion of the among-species variation in COT_{min} is explained by differences in size between species, with the relationship between COT_{min} and body mass shown to be negative indicating that per unit mass larger animals have a lower COT_{min} (Taylor et al., 1970; Schmidt-Nielsen 1972a; Full 1989). There are a number of mechanistic investigations discussing the biomechanical and kinematic factors that underlie the relationship between body mass and COT_{min} . Kram and Taylor (1990) provide evidence based on five mammal species that COT_{min} is determined primarily by the energy cost to the animal of

supporting its body weight and the duration over which the force for doing so is applied to the ground. This manifests as the length of an animal's step during pedestrian locomotion, which is positively related to its body size, being an important determinant of the energy cost of running. Subsequently, Pontzer (2007) showed that the length of the limb as a mechanical strut (effective limb length) is the primary anatomical driver of locomotor costs in terrestrial animals (see also Reilly et al. 2007). Very recently, Pontzer has demonstrated that unifying work- and force-based models centered on muscle metabolism enhances predictions of COT_{min} , not only for running on the flat but also up and down hills, and vertical climbing (Pontzer 2016).

Once the pervasive effect of body mass on COT_{min} is accounted for, however, considerable variation remains. The strength of the logged relationship between COT_{min} and body mass belies the absolute size of many of the residuals; species of similar body mass can have values of COT_{min} that differ by severalfold (Full 1989; Full et al. 1990; Kram 2012). This represents a huge difference in the cost of two similarly sized animals to move a given distance. Indeed, Pontzer's mechanistic model explains 95% of the variance in COT_{min} (Pontzer 2016); yet assessment of data points digitized from Figure 2c in that paper suggests that this impressive relationship still includes up to fivefold mass-independent differences in absolute COT_{min} for level running alone. For example, the COT_{min} for young lions *Panthera leo* (0.36 mL/kg/m) is calculated to be fourfold higher than that of similarly sized reindeer *Rangifer tarandus* calves (0.09 mL/kg/m; Chassin et al. 1976; Fancy and White 1985; Luick and White 1986). Although Chassin et al. (1976) were unable to account for the high cost of movement in lions, they suggested it may offer a physiological explanation for the reliance of lions on social hunting, which can increase the energy efficiency of obtaining food, in part because larger prey can be killed providing an energy return for multiple individuals in the pride (Williams et al. 2014).

However, it is challenging to infer adaptation from the study of single or small numbers of species because species may differ from one another for a large number of reasons that may or may not be related to the hypothesis of interest (Garland and Adolph 1994). The problems generated by comparisons of small numbers of species are exemplified by considering the COT_{min} of African hunting dogs *Lycaon pictus* (Taylor et al. 1971). Unlike lions, which as mentioned earlier have a relatively high COT_{min} , the COT_{min} of African hunting dogs (0.294 mL/kg/m) is very close to that predicted by their body mass (0.290 mL/kg/m; calculated for a mass of 8.75 kg using the parameter estimates in Table 1). This observation suggests that the evolution of social hunting is not always associated with high COT_{min} , which calls into question

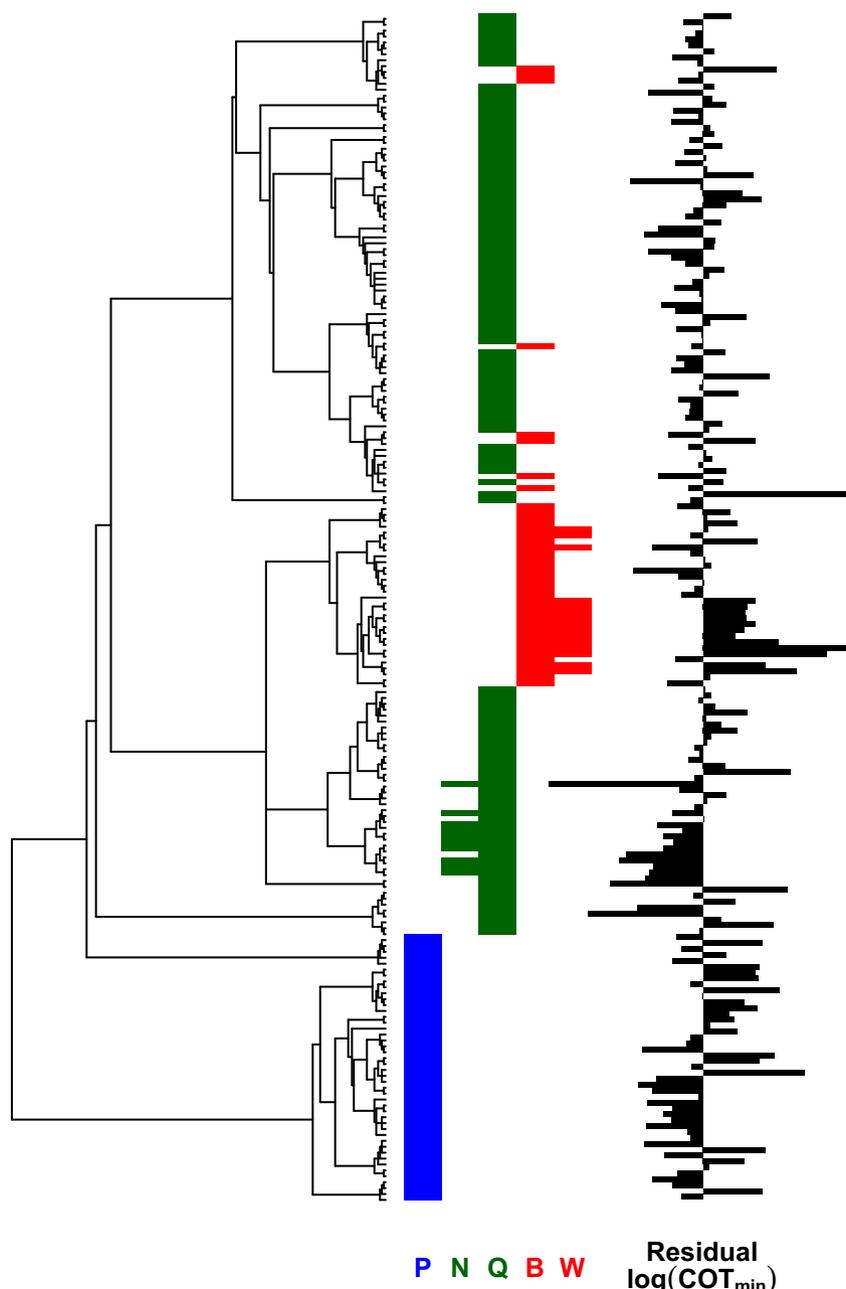


Figure 2. Phylogenetic distribution of polypedalism (P, blue), quadrupedalism (Q, green; specifically nocturnal lizards, N) and bipedalism (B, red; specifically waddling species, W), and mass-independent residual COT_{min} (black bars). Residual COT_{min} was calculated using the intercept and parameter estimate for body mass from Table 1.

the aforementioned hypothesis put forward by Chassin *et al.* (1976) that social hunting in lions evolved in part because of their high locomotion costs.

Phylogenetically informed comparative analyses offer a strong approach to inferring adaptation by testing for associations among traits across many species while explicitly taking evolutionary history into account (Rezende and Diniz-Filho 2012). Such analyses seek to reveal the selection pressures that have driven the evolution of interspecies differences and thereby offer an approach that is complementary to biomechanical investigations which

reveal the proximate mechanisms by which species achieve these differences. Although the interspecific relationship between body size and the energetics of locomotion has been well studied for more than 40 years (e.g., Taylor *et al.*, 1970; Schmidt-Nielsen 1972a; Full *et al.*, 1990; Pontzer 2007; White *et al.* 2008a; Halsey and White 2012), few investigations have examined the scaling of COT_{min} in a phylogenetic context, and those studies including phylogeny have had a narrow taxonomic focus (lizards: Autumn *et al.* 1997; Hare *et al.* 2007; mammals: Halsey and White 2012; birds: White *et al.* 2008a).

Table 1. Parameter estimates for, and importance of, the effects of body mass (M , kg), animals that are bipedal and animals that waddle on \log_{10} -transformed minimum cost of transport (mL/kg/m) for ectothermic and endothermic animals, assessed by phylogenetic least squares (maximum likelihood $\lambda = 0$ [95% CI: NA, 0.42], $r^2 = 0.85$). Importance is calculated as a sum of the Akaike weights over all of the models in which the term appears (see text for details).

Term	Estimate	SE	t	Importance
Intercept	-0.28	0.02	-12.85	
$\log_{10}M$	-0.28	0.01	-32.3	1
Waddle	0.31	0.08	4.01	1
Bipedal	-0.002	0.052	-0.03	0.26

In this study, taking advantage of the many relatively recent publications as well as previously compiled data sets to maximize sample size and species diversity, we use phylogenetically informed comparative analyses to test for differences in COT_{\min} between various groupings of terrestrial animals that use pedestrian locomotion for movement. Our aim was to identify groups that exhibit different COT_{\min} from the typical for terrestrial animals, through examination and quantification of the scaling relationships. We seek to complement proximate mechanistic explanations of COT_{\min} variability with ultimate, eco-evolutionary explanations. We test for differences between groups explored previously (two vs. many legs; Full 1989). We also test for differences in COT_{\min} between waddling and nonwaddling species, a comparison that has also been investigated previously. Fedak et al. (1974) and Pinshow et al. (1977) reported higher transport costs in waddling birds; yet, these analyses and others have considered small samples of species and thus provide only limited evidence that waddling is an expensive form of pedestrian locomotion. Furthermore, a recent phylogenetically informed comparison of cormorants *Phalacrocorax carbo*, another species that waddles, with running birds (Galliformes and Struthioniformes) found no significant difference in COT_{\min} (White et al. 2008a). We also test the nocturnality hypothesis, which suggests that night-active lizards are often moving around at low and suboptimal temperatures and will have decreased COT_{\min} to overcome the handicap that at lower temperatures, energy is applied to locomotion less efficiently (Autumn et al. 1994, 1997, 1999; Hare et al. 2007). The nocturnality hypothesis is supported by observations of low values of COT_{\min} for nocturnal geckos and skinks compared to other species of lizard both closely and distantly related (Autumn et al. 1994, 1997, 1999; Hare et al. 2007); however, an analysis including several nocturnal lizards together has not been undertaken. Furthermore, studies that manipulate temperature and measure the consequences of this for the COT_{\min} of ectotherms report

that COT_{\min} is independent of temperature (e.g., Moberly 1968; Herreid et al. 1981; John-Alder et al. 1983; Bennett and John-Alder 1984; Lighton et al. 1993), casting doubt on the nocturnality hypothesis. We investigate the nocturnality hypothesis by testing for an effect in ectotherms of temperature on COT_{\min} to determine whether species active at low body temperatures have high COT_{\min} , as well as testing for differences in COT_{\min} between nocturnal lizards and other ectotherms.

Material and Methods

Data for COT_{\min} were compiled from the peer-reviewed literature and were included only if data for body mass were also available. All data used in this study are available on ResearchGate. COT_{\min} was included if the authors of the original study calculated it as the slope of a linear regression relating metabolic rate and locomotion speed or provided data from which this slope could be calculated. The relationship between metabolic rate and locomotion speed is close to linear for most species, but not for all, and thus, we visually assessed the linearity of each data set. At high speeds, metabolic rate is independent of speed for large macropods (e.g., Dawson and Taylor 1973; Baudinette et al. 1992); so, for these species, COT_{\min} was calculated as the slope of a linear regression relating metabolic rate and locomotion speed for speeds below that at which metabolic rate becomes independent of speed. Both COT_{\min} and body mass were \log_{10} -transformed for analysis. In total, we compiled data for 201 species (eight amphibians, five arachnids, 31 birds, four crustaceans, 36 insects, 83 mammals, 34 nonavian reptiles; Fig. 2 and Table in Appendix S1). Sex differences in COT_{\min} have been documented for some species (e.g., Browning et al. 2006; Rezende et al. 2006; Lees et al. 2012), but not others (e.g., Shillington and Peterson 2002; Rose et al. 2014), and most studies do not report COT_{\min} for males and females separately; we therefore pooled data for males and females. Data were analyzed using phylogenetic generalized least squares (PGLS; Grafen 1989; Martins and Hansen 1997; Garland and Ives 2000) using the “ape” v3.1-1 (Paradis et al. 2004) and “caper” v0.5.2 (Orme et al. 2013) packages of R v3.0.2 (R Core Team, 2013). The tree used for analysis was constructed using published trees for mammals (Bininda-Emonds et al. 2007), birds (Jetz et al. 2012), amphibians (Pyron and Wiens 2011), reptiles (Pyron et al. 2013), and insects (Kambhampati 1995; Ward 2007; Misof et al. 2014), supplemented with additional information from tolweb.org (the full tree is provided as the Supporting Information). For birds, a single majority rule consensus tree was constructed from the published posterior distribution of 10,000 trees (Jetz et al. 2012) using “ape” v3.1-1 (Paradis

et al. 2004). Because the branch lengths in the various trees were provided in different units or not provided at all, Grafen's (1989) arbitrary branch length transformation was used (branch lengths set to a length equal to the number of descendant tips minus one). A measure of phylogenetic correlation, λ (Pagel 1999), was estimated by fitting PGLS models with different values of λ and finding the value that maximizes the log likelihood. The degree to which trait evolution deviates from Brownian motion ($\lambda = 1$) was determined by modifying the covariance matrix using the maximum likelihood value of λ , which is a multiplier of the off-diagonal elements of the covariance matrix (i.e., those quantifying the degree of relatedness between species).

For the full data set, the effects of body mass, bipedalism (bipedal or not), and waddling on COT_{\min} were examined. We define waddling following (Pinshow *et al.* 1977) as awkward gaits where the body undergoes large lateral displacements during locomotion and consider waddling species as members of the Anseriformes (ducks, geese, swans, screamers, and the magpie goose), Suliformes (frigate birds, gannets and boobies, cormorants and shags, and darters), Procellariiformes (albatrosses, petrels and shearwaters, storm petrels, and diving petrels), and Sphenisciformes (penguins). For ectotherms, the effects of body temperature and nocturnality (nocturnal lizard, or not) on COT_{\min} were also examined. Differences in COT_{\min} between nocturnal and non-nocturnal endotherms were not examined because, in contrast to ectotherms, nocturnal endotherms are not expected to be active at lower body temperatures than non-nocturnal endotherms.

We estimated the relative importance of size, waddling, and bipedalism (for the full data set) or size, body temperature, and nocturnality (for the ectotherm data set) by fitting models with all possible additive combinations of these predictors and comparing the models within these candidate sets on the basis of the second-order version of Akaike's information criterion (AIC_c) as a measure of model fit (Burnham and Anderson 2010). The relative importance weight of each predictor was calculated by summing the Akaike weights (w_i , the relative likelihood of the model compared with all others: the likelihood of the model divided by the sum of the likelihoods of all other models) of the models containing the predictor (e.g., the relative importance of body mass was calculated by summing the values of w_i of all models that contained body mass as a predictor; Burnham and Anderson 2010). Relative importance (Σw_i) represents the probability that a given predictor is a component of the best model of the candidate set (Symonds and Moussalli 2011), but should not be interpreted as a threshold metric used to separate weak, moderate, or strong support for predictors because

Σw_i can take a wide range of values even when predictor variables are unrelated to the response (Galipaud *et al.* 2014). We therefore interpret Σw_i conservatively, concluding that predictors with $\Sigma w_i = 1$ have an influence on COT_{\min} , and interpreting predictors with $\Sigma w_i < 1$ based on the magnitude of their estimated biological effect on COT_{\min} .

Results

With data for all species included, there was an effect of body mass on COT_{\min} ($\Sigma w_i = 1.00$, Fig. 3, Table 1), and a residual difference between waddling bipedal species and all other species ($\Sigma w_i = 1$; waddling species have an COT_{\min} that is about twofold higher than other species, Fig. 3, Table 1). However, there was essentially no difference between bipedal species in general and other species ($\Sigma w_i = 0.26$; bipedal species have a mean COT_{\min} that differs from nonbipedal species of similar mass by <1%; Fig. 3, Table 1).

When only data for ectotherms were considered, there was an effect of body mass ($\Sigma w_i = 1.00$, Table 2) and a difference between nocturnal lizards and other ectotherms ($\Sigma w_i = 0.91$; nocturnal lizards have a mean COT_{\min} that is 47% of that for other ectotherms of similar mass: Fig. 3, Table 2). There was only a small effect of temperature on COT_{\min} ($\Sigma w_i = 0.41$; mean COT_{\min} of ectotherms decreases by $\sim 2\%/^{\circ}\text{C}$: Table 2, Fig. 4).

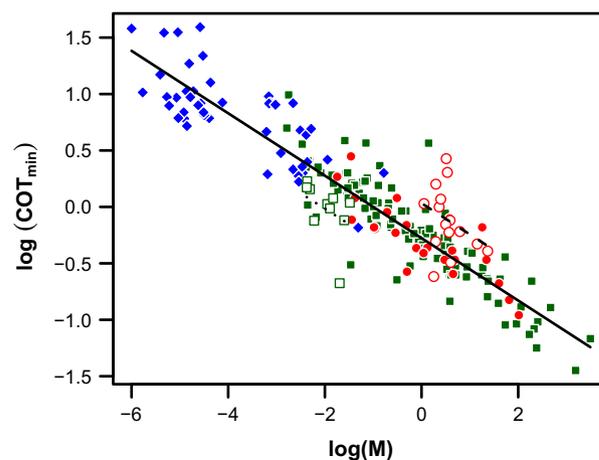


Figure 3. Scaling of \log_{10} -transformed cost of transport (COT_{\min} , mL/kg/m) with \log_{10} -transformed body mass (M , kg) in bipedal (red circles), quadrupedal (green squares), and polypedal (blue diamonds) species; unfilled red symbols represent waddling species and unfilled green symbols represent nocturnal lizards. The dashed and solid lines represent the relationship between COT_{\min} and mass for waddling and all remaining species, respectively (Table 1); the dotted line represents the relationship for nocturnal lizards (Table 2).

Table 2. Parameter estimates and importance for the effects of body mass (M, kg), body temperature (°C), and nocturnality on \log_{10} -transformed minimum cost of transport (mL/kg/m) for ectothermic animals, assessed by phylogenetic generalized least squares (maximum likelihood $\lambda = 0$ [95% CI: NA, 0.67], $r^2 = 0.79$). Importance is calculated as a sum of the Akaike weights over all of the models in which the term appears (see text for details).

Term	Estimate	SE	<i>t</i>	Importance
Intercept	0.07	0.17	0.40	
$\log_{10}M$	-0.27	0.02	-14.4	1
Nocturnality	-0.32	0.09	-3.52	0.91
Temperature	-0.007	0.006	-1.23	0.41

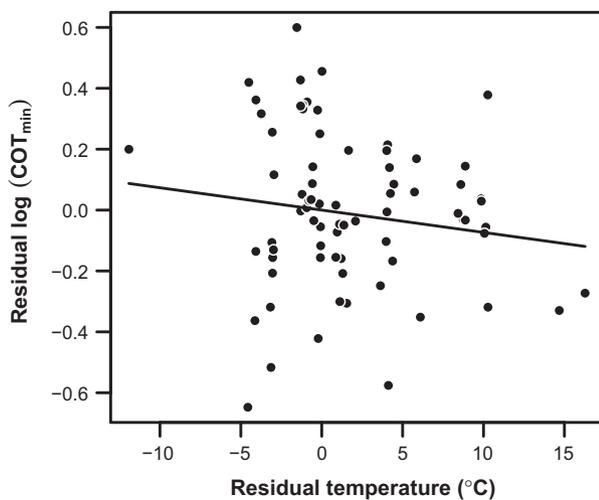


Figure 4. The among-species relationship between body temperature (°C) and minimum cost of transport (COT_{min}) for ectotherms. Temperature and COT_{min} are presented as residuals to account for the influence of other predictors on COT_{min} (Table 2). The solid line represents the parameter estimate for the effect of temperature from Table 2, plotted through the origin (0,0).

Discussion

As shown in the present study (Fig. 3) and others (e.g., Schmidt-Nielsen 1972a; Full *et al.*, 1990), COT_{min} for leg-based movement on land decreases with increasing size. The negative relationship between COT_{min} and size across species, which has an allometric scaling exponent of -0.28 , probably arises mainly because small animals have higher stride frequencies than large ones (Heglund and Taylor 1988; Gatesy and Biewener 1991) and therefore have less time available during each stride to generate force against the ground (Kram and Taylor 1990). High rates of force generation require the recruitment of faster, less economical muscle fibers (Huxley 1974; Rall 1985; Kram and Taylor 1990; Griffin and Kram 2000) and perhaps also the generation of force more quickly than is

optimal for those fibers that are activated (Bárány 1967), thereby increasing COT_{min} .

However, animals of a similar size present in our data set exhibit considerable variation in their energy economy (Figs. 2, 3), routinely representing sevenfolds of difference. Some of these differences in COT_{min} may be explained by certain species running relatively poorly on a treadmill, the use of juvenile animals, measurement error, and the assumption of perfect linearity in the derivation of COT_{min} . However, much of the variation is likely to be genuine, and these among-species differences have been proposed as important in the evolution of a range of ecological patterns. Our study confirms and progresses understanding of which eco-evolutionary traits independent of body mass are associated with COT_{min} . Our phylogenetically informed analysis across 201 terrestrial species confirmed the lack of evidence for a difference in COT_{min} between species with two legs and species with more, which fits with the present biomechanical theories that locomotor costs are driven by supporting body weight (Kram and Taylor 1990) and moderated by step, limb, and limb muscle length (Kram and Taylor 1990; Roberts *et al.* 1998a,b; Pontzer 2007). Our analyses also adds considerable weight to the relatively limited previous evidence that waddling bipeds have a higher COT_{min} than do other animals (Fig. 3, Table 1), indicating that it is approximately double. It has previously been suggested that the ultimate explanation for this greater COT_{min} may be that waddling species such as penguins, ducks, geese, and cormorants have evolved short legs in association with aquatic specialization (White *et al.* 2008a). Thus, from a proximate biomechanical standpoint, the cost of generating force probably also explains the generally high COT_{min} in waddling bipeds, because their short legs necessitate high rates of force generation during short strides (Griffin and Kram 2000; see also Pontzer 2007). An interesting avenue for further work would therefore be to determine whether additional residual variation in COT_{min} can be explained by among-species differences in the time course of force generation. Furthermore, within ectotherms, we found support for the nocturnality hypothesis (Autumn *et al.* 1994, 1997, 1999; Hare *et al.* 2007), suggesting that poikilothermic species of lizard which forage at night are substantially more energetically economic than other ectotherm species (our analyses suggest their COT_{min} is about half), although there was little support for the related hypothesis that COT_{min} changes with body temperature (Table 2, Fig. 4).

The lack of a relationship between COT_{min} and temperature in ectotherms is consistent with the results of all single-species studies that we are aware of (e.g., Moberly 1968; Herreid *et al.* 1981; John-Alder *et al.* 1983; Bennett and John-Alder 1984; Lighton *et al.* 1993). Furthermore,

the parameter estimate for temperature corresponding to a 20% decrease in COT_{min} per 10°C of temperature increase has low precision and is small compared to the 1.5- to threefold changes in physiological rates that are typically caused by acute 10°C changes in temperature (Seebacher *et al.* 2015). The finding that COT_{min} is largely independent of body temperature (Table 2) despite the profound effect of temperature on rates of physiological processes (Dell *et al.* 2011) again supports the hypothesis that COT_{min} is influenced primarily by the cost of generating force to support the body against gravity (Kram and Taylor 1990). Furthermore, this finding goes against the nocturnality hypothesis, which suggests that nocturnal lizards, which evolved from diurnal species active at high body temperatures, are often active at low and suboptimal temperatures and therefore have decreased COT_{min} to overcome the reduced performance observed at low temperatures (Autumn *et al.* 1994, 1997, 1999; Hare *et al.* 2007). Despite this, the probability that the nocturnality predictor is present in the best model in the candidate set of our analysis is 0.91 and nocturnal lizards have a mean COT_{min} that is 47% of the COT_{min} of other ectotherms of similar mass (Fig. 3, Table 2). This is fairly clear evidence that nocturnal lizards have a low COT_{min} . Intriguingly, though, the low COT_{min} is unlikely to arise as a consequence of selection acting to ameliorate temperature-mediated changes in COT_{min} directly, as proposed by the nocturnality hypothesis, because COT_{min} is independent of body temperature. Instead, the changes in COT_{min} must arise as a correlated response to selection on other traits. Maximum aerobic metabolic rate is typically thermally dependent at low temperatures in reptiles (e.g., Bennett 1982; Autumn *et al.* 1994; White *et al.* 2008b); so, all else being equal, decreases in temperature will therefore lead to reductions in the maximum speed that can be sustained aerobically. Selection to reduce COT_{min} or increase aerobic capacity should overcome this limitation of low-temperature activity (Autumn *et al.* 1994). A future avenue for research should be to investigate the physiological and/or biomechanical underpinnings that enable this energy economy in nocturnal lizards; again, we suggest prioritizing investigation of limb length and the time course of force generation.

Conflict of Interest

None declared.

References

Autumn, K., R. B. Weinstein, and R. J. Full. 1994. Low cost of locomotion increases performance at low temperature in a nocturnal lizard. *Physiol. Zool.* 67:238–262.

- Autumn, K., C. T. Farley, M. Emshwiller, and R. J. Full. 1997. Low cost of locomotion in the banded gecko: a test of the nocturnality hypothesis. *Physiol. Zool.* 70:660–669.
- Autumn, K., D. Jindrich, D. Denardo, and R. Mueller. 1999. Locomotor performance at low temperature and the evolution of nocturnality in geckos. *Evolution* 53:580–599.
- Bárány, M. 1967. ATPase activity of myosin correlated with speed of muscle shortening. *J. Gen. Physiol.* 50:197–218.
- Baudinette, R. V., G. K. Snyder, and P. B. Frappell. 1992. Energetic cost of locomotion in the tammar wallaby. *Am. J. Physiol.* 262:R771–R778.
- Bennett, A. F. 1982. Energetics of activity in reptiles. Pp. 155–199 in C. Gans and F. H. Pough, eds. *Biology of the reptilia*. Academic Press, New York, NY.
- Bennett, A. F., and H. B. John-Alder. 1984. The effect of body temperature on the locomotory energetics of lizards. *J. Comp. Physiol. B.* 155:21–27.
- Bininda-Emonds, O. R. P., M. Cardillo, K. E. Jones, R. D. E. Macphee, R. M. D. Beck, R. Grenyer, *et al.* 2007. The delayed rise of present-day mammals. *Nature* 446:507–512.
- Browning, R. C., E. A. Baker, J. A. Herron, and R. Kram. 2006. Effects of obesity and sex on the energetic cost and preferred speed of walking. *J. Appl. Physiol.* 100:390–398.
- Burnham, K. P., and D. R. Anderson. 2010. *Model selection and multi-model inference: a practical information-theoretic approach*. Springer, New York, NY.
- Calder, W. A. III. 1984. *Size, function, and life history*. Harvard Univ. Press, Cambridge, U.K.
- Chassin, P. S., C. R. Taylor, N. C. Heglund, and H. J. Seeherman. 1976. Locomotion in lions: energetic cost and maximum aerobic capacity. *Physiol. Zool.* 49:1–10.
- Dawson, T. J., and C. R. Taylor. 1973. Energetic cost of locomotion in kangaroos. *Nature* 246:313–314.
- Dell, A. I., S. Pawar, and V. M. Savage. 2011. Systematic variation in the temperature dependence of physiological and ecological traits. *Proc. Natl Acad. Sci. USA* 108:10591–10596.
- Fancy, S. G., and R. G. White. 1985. Incremental cost of activity. Pp. 143–159 in R. J. Hudson and R. G. White, eds. *Bioenergetics of wild herbivores*. CRC Press, Boca Raton, FL.
- Fedak, M. A., B. Pinshow, and K. Schmidt-Nielsen. 1974. Energy cost of bipedal running. *Am. J. Physiol.* 227:1038–1044.
- Full, R. J. 1989. Mechanics and energetics of terrestrial locomotion: from bipeds to polypeds. Pp. 175–182 in W. Wieser and E. Gnaiger, eds. *Energy transformations in cells and animals*. Georg Thieme Verlag, Stuttgart.
- Full, R., D. Zuccarello, and A. Tullis. 1990. Effect of variation in form on the cost of terrestrial locomotion. *J. Exp. Biol.* 150:233–246.
- Galipaud, M., M. A. F. Gillingham, M. David, and F.-X. Dechaume-Moncharmont. 2014. Ecologists overestimate the importance of predictor variables in model averaging: a plea for cautious interpretations. *Methods Ecol. Evol.* 5:983–991.

- Garland, T., Jr 1983. Scaling the ecological cost of transport to body mass in terrestrial mammals. *Am. Nat.* 121:571–587.
- Garland, T., Jr, and S. C. Adolph. 1994. Why not to do two species comparative studies: limitations on inferring adaptation. *Physiol. Biochem. Zool.* 67:797–828.
- Garland, T., Jr, and A. R. Ives. 2000. Using the past to predict the present: confidence intervals for regression equations in phylogenetic comparative methods. *Am. Nat.* 155:346–364.
- Gatesy, S., and A. Biewener. 1991. Bipedal locomotion: effects of speed, size and limb posture in birds and humans. *J. Zool.* 224:127–147.
- Gefen, E. 2011. The relative importance of respiratory water loss in scorpions is correlated with species habitat type and activity pattern. *Physiol. Biochem. Zool.* 84:68–76.
- Grafen, A. 1989. The phylogenetic regression. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 326:119–157.
- Griffin, T. M., and R. Kram. 2000. Penguin waddling is not wasteful. *Nature* 408:929.
- Halsey, L. G. 2013. The relationship between energy expenditure and speed during pedestrian locomotion in birds: a morphological basis for the elevated y -intercept? *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* 165:295–298.
- Halsey, L. G., and C. R. White. 2012. Comparative energetics of mammalian locomotion: humans are not different. *J. Hum. Evol.* 63:718–722.
- Halsey, L. G., P. G. D. Matthews, E. L. Rezende, L. Chauvaud, and A. A. Robson. 2015. The interactions between temperature and activity levels in driving metabolic rate: theory, with empirical validation from contrasting ectotherms. *Oecologia* 177:1117–1129.
- Halsey, L. 2016. Terrestrial movement energetics: current knowledge and its application to the optimising animal. *J. Exp. Biol.* 219:1424–1431.
- Hare, K. M., S. Pledger, M. B. Thompson, J. H. Miller, and C. H. Daugherty. 2007. Low cost of locomotion in lizards that are active at low temperatures. *Physiol. Biochem. Zool.* 80:46–58.
- Heglund, N. C., and C. R. Taylor. 1988. Speed, stride, frequency and energy cost per stride: how do they change with body size and gait? *J. Exp. Biol.* 138:301–318.
- Herreid, C. F., R. J. Full, and D. A. Prawel. 1981. Energetics of cockroach locomotion. *J. Exp. Biol.* 94:189–202.
- Huxley, A. F. 1974. Muscular contraction. *J. Physiol.* 243:1–43.
- Jetz, W., G. H. Thomas, J. B. Joy, K. Hartmann, and A. O. Mooers. 2012. The global diversity of birds in space and time. *Nature* 491:444–448.
- John-Alder, H. B., C. H. Lowe, and A. F. Bennett. 1983. Thermal dependence of locomotory energetics and aerobic capacity of the gila monster *Heloderma suspectum*. *J. Comp. Physiol. B.* 151:119–126.
- Kambhampati, S. 1995. A phylogeny of cockroaches and related insects based on DNA sequence of mitochondrial ribosomal RNA genes. *Proc. Natl Acad. Sci. USA* 92:2017–2020.
- Kram, R. 2012. Taylor's treadmill menagerie. *J. Exp. Biol.* 215:2349–2350.
- Kram, R., and C. R. Taylor. 1990. Energetics of running: a new perspective. *Nature* 346:265–267.
- Lees, J. J., R. L. Nudds, L. P. Folkow, K.-A. Stokkan, and J. R. Codd. 2012. Understanding sex differences in the cost of terrestrial locomotion. *Proc. R. Soc. Lond. B Biol. Sci.* 279:826–832.
- Lighton, J. R. B., and L. G. Halsey. 2011. Flow-through respirometry applied to chamber systems: pros and cons, hints and tips. *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* 158:265–275.
- Lighton, J. R. B., J. A. Weier, and D. H. Feener. 1993. The energetics of locomotion and load carriage in the desert harvester ant *Pogonomyrmex rugosus*. *J. Exp. Biol.* 181:49–61.
- Luick, B. R., and R. G. White. 1986. Oxygen consumption for locomotion by caribou calves. *J. Wildl. Manage.* 50:148–152.
- Martins, E. P., and T. F. Hansen. 1997. Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. *Am. Nat.* 149:646–667.
- Misof, B., S. Liu, K. Meusemann, R. S. Peters, A. Donath, C. Mayer, et al. 2014. Phylogenomics resolves the timing and pattern of insect evolution. *Science* 346:763–767.
- Moberly, W. R. 1968. The metabolic responses of the common iguana, *Iguana iguana*, to walking and diving. *Comp. Biochem. Physiol.* 27:21–32.
- Orme, D., R. P. Freckleton, G. H. Thomas, Y. Petzoldt, S. Fritz, N. Isaac, et al. 2013. caper: Comparative Analyses of Phylogenetics and Evolution in R. R package version 0.5.2. ed.
- Pagel, M. 1999. Inferring the historical patterns of biological evolution. *Nature* 401:877–884.
- Paradis, E., J. Claude, and K. Strimmer. 2004. APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* 20:289–290.
- Pinshow, B., M. A. Fedak, and K. Schmidt-Nielsen. 1977. Terrestrial locomotion in penguins: it costs more to waddle. *Science* 195:592–594.
- Pontzer, H. 2007. Effective limb length and the scaling of locomotor cost in terrestrial animals. *J. Exp. Biol.* 210:1752–1761.
- Pontzer, H. 2016. A unified theory for the energy cost of legged locomotion. *Biol. Lett.* 12: 20150935. <http://dx.doi.org/10.1098/rsbl.2015.0935>
- Pyron, R. A., and J. J. Wiens. 2011. A large-scale phylogeny of Amphibia including over 2800 species, and a revised classification of extant frogs, salamanders, and caecilians. *Mol. Phylogenet. Evol.* 61:543–583.
- Pyron, R. A., F. T. Burbrink, and J. J. Wiens. 2013. A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. *BMC Evol. Biol.* 13:93.

- R Core Team. 2013. R: a language and environment for statistical computing. 3.0.0 ed. R Foundation for Statistical Computing, Vienna, Austria.
- Rall, J. A. 1985. Energetic aspects of skeletal muscle contraction: implications of fiber types. *Exerc. Sport Sci. Rev.* 13:33–74.
- Reilly, S. M., E. J. McElroy, and A. R. Biknevicius. 2007. Posture, gait and the ecological relevance of locomotor costs and energy-saving mechanisms in tetrapods. *Zoology (Jena)* 110:271–289.
- Rezende, E. L., and J. A. F. Diniz-Filho. 2012. Phylogenetic analyses: comparing species to infer adaptations and physiological mechanisms. *Compr. Physiol.* 2:639–674.
- Rezende, E. L., S. A. Kelly, F. R. Gomes, M. A. Chappell, and T. Garland Jr. 2006. Effects of size, sex, and voluntary running speeds on costs of locomotion in lines of laboratory mice selectively bred for high wheel-running activity. *Physiol. Biochem. Zool.* 79:83–99.
- Rezende, E. L., F. R. Gomes, M. A. Chappell, and T. Garland Jr. 2009. Running behavior and its energy cost in mice selectively bred for high voluntary locomotor activity. *Physiol. Biochem. Zool.* 82:662–679.
- Roberts, T., R. Kram, P. Weyand, and C. R. Taylor. 1998a. Energetics of bipedal running. I. Metabolic cost of generating force. *J. Exp. Biol.* 201:2745–2751.
- Roberts, T. J., M. S. Chen, and C. R. Taylor. 1998b. Energetics of bipedal running. II. Limb design and running mechanics. *J. Exp. Biol.* 201:2753–2762.
- Rose, K. A., P. G. Tickle, J. J. Lees, K.-A. Stokkan, and J. R. Codd. 2014. Neither season nor sex affects the cost of terrestrial locomotion in a circumpolar diving duck: the common eider (*Somateria mollissima*). *Polar Biol.* 37:879–889.
- Scantlebury, D. M., M. G. L. Mills, R. P. Wilson, J. W. Wilson, M. E. J. Mills, S. M. Durant, et al. 2014. Flexible energetics of cheetah hunting strategies provide resistance against kleptoparasitism. *Science* 346:79–81.
- Schmidt-Nielsen, K. 1972a. Locomotion: energy cost of swimming, flying and running. *Science* 172:222–228.
- Schmidt-Nielsen, K. 1972b. Locomotion: energy cost of swimming, flying, and running. *Science* 177:222–228.
- Schmidt-Nielsen, K. 1984. *Scaling: why is animal size so important?*. Cambridge Univ. Press, Cambridge, U.K.
- Seebacher, F., C. R. White, and C. E. Franklin. 2015. Physiological plasticity increases resilience of ectothermic animals to climate change. *Nat. Clim. Chang.* 5:61–66.
- Shillington, C., and C. C. Peterson. 2002. Energy metabolism of male and female tarantulas (*Aphonopelma anax*) during locomotion. *J. Exp. Biol.* 205:2909–2914.
- Speakman, J. R., and C. Selman. 2003. Physical activity and resting metabolic rate. *Proc. Nutr. Soc.* 62:621–634.
- Symonds, M. R. E., and A. Moussalli. 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behav. Ecol. Sociobiol.* 65:13–21.
- Taylor, C., K. Schmidt-Nielsen, and J. Raab. 1970. Scaling of energetic cost of running to body size in mammals. *Am. J. Physiol.* 219:1104–1107.
- Taylor, C. R., K. Schmidt-Nielsen, R. Dmi'el, and M. A. Fedak. 1971. Effect of hyperthermia on heat balance during running in the African hunting dog. *Am. J. Physiol.* 220:823–827.
- Taylor, C., N. Heglund, and G. Maloiy. 1982. Energetics and mechanics of terrestrial locomotion. I. Metabolic energy consumption as a function of speed and body size in birds and mammals. *J. Exp. Biol.* 97:1–21.
- Ward, P. S. 2007. Phylogeny, classification, and species-level taxonomy of ants (Hymenoptera: Formicidae). *Zootaxa* 1668:549–563.
- White, C. R., and M. R. Kearney. 2014. Metabolic scaling in animals: methods, empirical results, and theoretical explanations. *Compr. Physiol.* 4:231–256.
- White, C. R., G. R. Martin, and P. J. Butler. 2008a. Pedestrian locomotion energetics and gait characteristics of a diving bird, the great cormorant, *Phalacrocorax carbo*. *J. Comp. Physiol. B.* 178:745–754.
- White, C. R., J. S. Terblanche, A. P. Kabat, T. M. Blackburn, S. L. Chown, and P. J. Butler. 2008b. Allometric scaling of maximum metabolic rate: the influence of temperature. *Funct. Ecol.* 22:616–623.
- White, C. R., D. Grémillet, J. A. Green, G. R. Martin, and P. J. Butler. 2011. Metabolic rate throughout the annual cycle reveals the demands of an Arctic existence in Great Cormorants. *Ecology* 92:475–486.
- Williams, T. M., L. Wolfe, T. Davis, T. Kendall, B. Richter, Y. Wang, et al. 2014. Instantaneous energetics of puma kills reveal advantage of felid sneak attacks. *Science* 346:81–85.

Supporting Information

Additional Supporting Information may be found online in the supporting information tab for this article:

Appendix S1. Full data set and phylogenetic information.