

A general scaling law reveals why the largest animals are not the fastest

Myriam R. Hirt^{1,2*}, Walter Jetz^{1,3,4}, Björn C. Rall^{1,2} and Ulrich Brose^{1,2}

Speed is the fundamental constraint on animal movement, yet there is no general consensus on the determinants of maximum speed itself. Here, we provide a general scaling model of maximum speed with body mass, which holds across locomotion modes, ecosystem types and taxonomic groups. In contrast to traditional power-law scaling, we predict a hump-shaped relationship resulting from a finite acceleration time for animals, which explains why the largest animals are not the fastest. This model is strongly supported by extensive empirical data (474 species, with body masses ranging from 30 µg to 100 tonnes) from terrestrial as well as aquatic ecosystems. Our approach unravels a fundamental constraint on the upper limit of animal movement, thus enabling a better understanding of realized movement patterns in nature and their multifold ecological consequences.

Movement is one of the most fundamental processes of life. The individual survival of mobile organisms depends on their ability to reach resources and mating partners, escape predators, and switch between habitat patches or breeding and wintering grounds. By creating and sustaining individual home ranges¹ and meta-communities², movement also profoundly affects the ability of animals to cope with changes in land use and in climate³. Additionally, movement determines encounter rates and thus the strength of species interactions⁴, which is an important factor influencing ecosystem stability⁵. Accordingly, a generalized and predictive understanding of animal movement is crucial^{6,7}.

A fundamental constraint on movement is maximum speed. The realized movement depends on ecological factors such as landscape structure, habitat quality or sociality, but the range within which this realized movement occurs meets its upper limit at maximum movement speed. Similar to many physiological and ecological parameters, movement speed of animals is often thought to follow a power-law relationship with body mass^{8–10}. However, scientists have always struggled with the fact that, in running animals, the largest are not the fastest^{11–14}. In nature, the fastest running or swimming animals such as cheetahs or marlins are of intermediate size, indicating that a hump-shaped pattern may be more realistic. There have been numerous attempts to describe this phenomenon^{11–13,15,16}. Although biomechanical and morphological models have been tailored to explain this within taxonomic groups^{14,16–18}, a general mechanistic model predicting the large-scale pattern (over the full body-mass range) across all taxonomic groups and ecosystem types is still lacking. Here, we fill this void with a maximum-speed model based on the concept that animals are limited in their time for maximum acceleration because of restrictions on the quickly available energy. Consequently, acceleration time becomes the critical factor determining the maximum speed of animals. In the following, we first develop the maximum-speed model (in equations that are illustrated in the conceptual Fig. 1), test the model predictions employing a global database and eventually illustrate its applications to advance a more general understanding of animal movement.

Results

Model development. Consistent with prior models^{8,10}, we start with a power-law scaling of theoretical maximum speed $v_{\max(\text{theor})}$ of animals with body mass M :

$$v_{\max(\text{theor})} = aM^b \quad (1)$$

During acceleration, the speed of an animal over time t saturates^{19–21} (Fig. 1a, solid lines) approaching $v_{\max(\text{theor})}$ (Fig. 1a, dotted lines):

$$v(t) = v_{\max(\text{theor})}(1 - e^{-kt}) \quad (2)$$

The acceleration constant k describes how fast an animal reaches $v_{\max(\text{theor})}$. In analogy to Newton's second law, the acceleration k should scale relative to the ratio between maximum force, F , and body mass, M : that is, $k \sim F/M$. Knowing that maximum muscle force roughly scales with body mass as $F \sim M^d$, this yields a general power-law scaling of k with body mass M :

$$k = cM^{d-1} \quad (3)$$

with constants c and d . As the allometric exponent d of the muscle force falls within the range 0.75 to 0.94 (refs. 14,22,23), the overall exponent $(d - 1)$ should be negative, implying that larger animals need more time to accelerate to the same speed than smaller ones (see conceptual Fig. 1a; colour code exemplifies four animals of different size). Note that this general scaling relationship also allows for the special cases of a constant acceleration across species or a linear relationship with body mass.

Whereas prolonged high speeds are related to the maximum aerobic metabolism, maximum burst speeds are linked to anaerobic capacity^{24,25}. For maximum aerobic speed, 'slow twitch' fibres are needed, which are highly efficient at using oxygen for generating adenosine triphosphate (ATP) to fuel muscle contractions. Thus, they produce energy more slowly but for a long period of time before they become fatigued, and they allow for continuous,

¹EcoNetLab, German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig 04103, Germany. ²EcoNetLab, Friedrich Schiller University Jena, Dornburger Strasse 159, 07743 Jena, Germany. ³Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT 06511, USA.

⁴Department of Life Sciences, Imperial College London, Silwood Park, Ascot SL5 7QN, UK. *e-mail: myriam.hirt@idiv.de

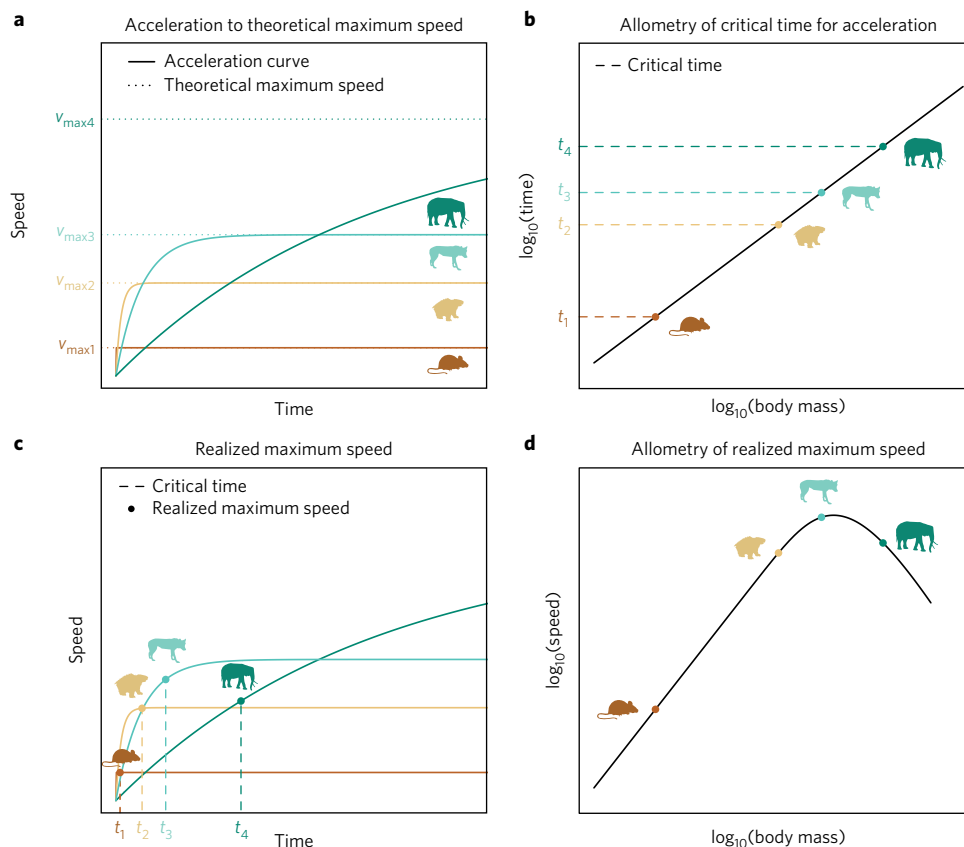


Figure 1 | Concept of time-dependent and mass-dependent realized maximum speed of animals. **a**, Acceleration of animals follows a saturation curve (solid lines) approaching the theoretical maximum speed (dotted lines) depending on body mass (colour code). **b**, The time available for acceleration increases with body mass following a power law. **c,d**, This critical time determines the realized maximum speed (**c**), yielding a hump-shaped increase of maximum speed with body mass (**d**).

extended muscle contractions. In contrast, maximum anaerobic speed is fuelled by a special type of ‘fast twitch’ fibres, which use ATP from the ATP storage of the fibre until it is depleted. Thus, they produce energy more quickly but also become fatigued very rapidly and only allow for short bursts of speed. As our maximum-speed model is based on this maximum anaerobic capacity, the critical time τ available for maximum acceleration is limited by the amount of fast twitch fibre and their energy storage capacity. This storage capacity is correlated with the amount of muscle tissue mass, which is directly linked to body mass. Thus, similar to the muscle tissue mass, τ should follow a power law:

$$\tau = fM^g \quad (4)$$

where the allometric exponent g should fall in the range 0.76 to 1.27 documented for the allometric scaling of muscle tissue mass^{26–29}. This power law implies that larger animals should have more time for acceleration (dashed lines in conceptual Fig. 1b, c). However, the power-law relationship of the critical time τ in our model allows for a negative or positive scaling of energy availability with body mass as well as the lack of a relationship (constant energy availability across body masses ($f=0$)). Although we have included power-law relationships of k and τ (equations (3) and (4)) in our model, these scaling assumptions are not strictly necessary. Instead, our only critical assumptions are that acceleration over time follows a saturation curve (equation (1)) and that the time available for anaerobic acceleration is limited.

Within the critical time τ , after which the energy available for acceleration is depleted, the animal reaches its realized maximum

speed v_{\max} (points in Fig. 1c), which may be lower than the theoretical maximum speed (Fig. 1a, dotted lines). Combining equations (1)–(4) with $t = \tau$ yields $v_{\max} = aM^b(1 - e^{-cfM^{d-1+g}})$ which simplifies to

$$v_{\max} = aM^b(1 - e^{-hM^i}) \quad (5)$$

where $i = d - 1 + g$ and $h = cf$. This equation predicts a hump-shaped relationship between realized maximum speed and body mass (conceptual Fig. 1d).

The limiting term $1 - e^{-hM^i}$ represents the fraction of the theoretical maximum speed that is realized and is defined on the interval $[0;1]$. For low body masses, this term is close to 1 and the realized maximum speed approximates the theoretical maximum. With increasing body masses, this term decreases and reduces the realized maximum speed. Put simply, small to intermediately sized animals accelerate quickly and have enough time to reach their theoretical maximum speed, whereas large animals are limited in acceleration time and run out of readily mobilizable energy before being able to reach their theoretically possible maximum. Therefore, they have a lower realized maximum speed than predicted by a power-law scaling relationship.

Test of model predictions by empirical database. To test the model predictions (Fig. 1d), we compiled literature data on maximum speeds of running, flying and swimming animals including not only mammals, fish and bird species but also reptiles, molluscs and arthropods. Body masses of these species range

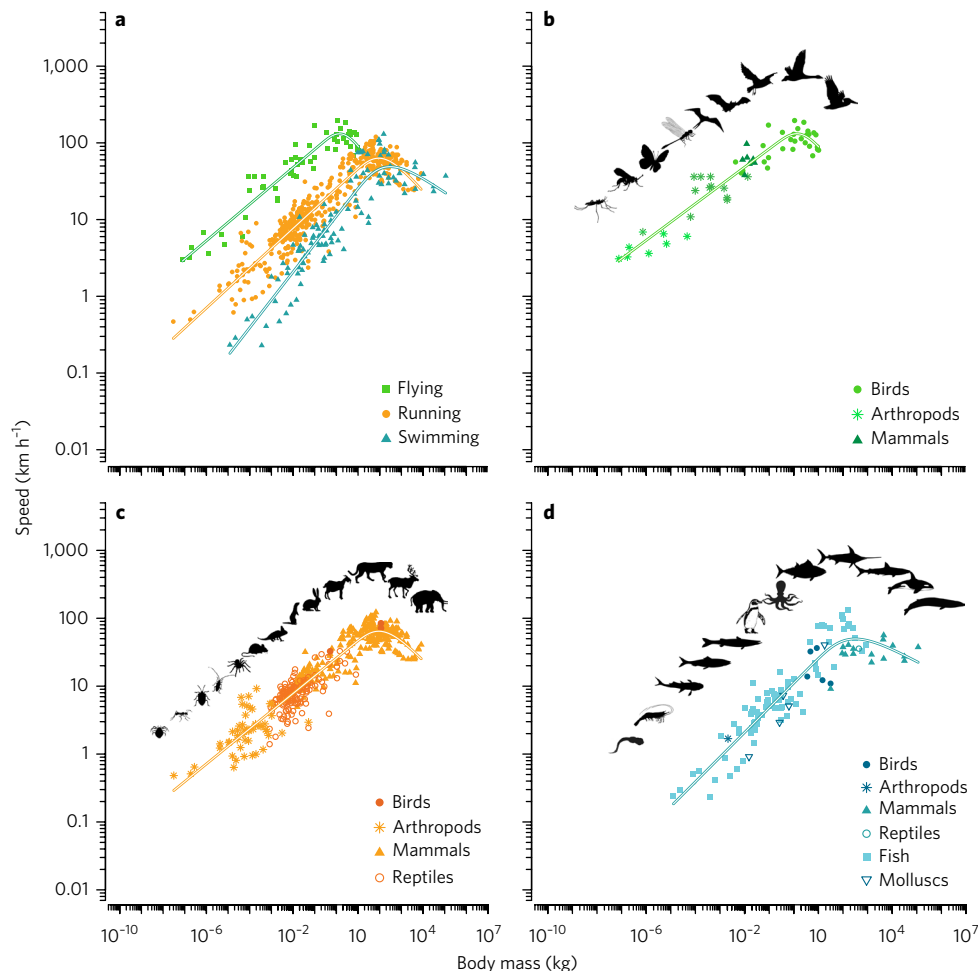


Figure 2 | Empirical data and time-dependent model fit for the allometric scaling of maximum speed. **a**, Comparison of scaling for the different locomotion modes (flying, running, swimming). **b–d**, Taxonomic differences are illustrated separately for flying (**b**; $n=55$), running (**c**; $n=458$) and swimming (**d**; $n=109$) animals. Overall model fit: $R^2=0.893$. The residual variation does not exhibit a signature of taxonomy (only a weak effect of thermoregulation; see Methods).

from 3×10^{-8} kg to 108,400 kg. Statistical comparison amongst multiple models (see Methods) shows that the time-dependent maximum-speed model is the most adequate (see Supplementary Table 3). Our model (Fig. 2, parameter values in Supplementary Table 4) shows that the initial power-law increase of speed with body mass is similar for running and flying animals ($b=0.26$ and 0.24 , respectively). However, flying animals are nearly six times as fast as running ones ($a=143$ and 26 , respectively). For swimming animals, the power-law increase in speed is steeper ($b=0.36$, Fig. 2a). This is because water is 800 times as dense and 60 times as viscous as air³⁰ (in which both flying and running animals move). Small aquatic animals are slower than running animals of the same body mass, whereas larger species approach a similar speed to that of their running equivalents. This implies that in water, body mass brings a greater benefit in gaining speed. The second exponent is lower for flying animals ($i=-0.72$) than for running ($i=-0.6$) and swimming ones ($i=-0.56$). Future research will need to disentangle the relative importance of anaerobic and musculoskeletal constraints on movement speed by measuring muscle force, muscle mass, body mass and maximum acceleration for the same species to narrow down this large range of possible exponents. Furthermore, this may allow us to address the systematic differences in the exponent i between the locomotion modes as well as potential morphological side effects

(for example quadrupedal versus bipedal running, or soaring versus flapping flight).

Although the model provides strikingly strong fits with observations ($R^2=0.893$), some unexplained variation remains. This might partially be explained by the fact that our data probably include not only maximum anaerobic speeds but also some slightly slower maximum aerobic speeds. Moreover, we assessed the robustness of our model by exploring this residual variation with respect to taxonomy (arthropods, birds, fish, mammals, molluscs, reptiles), primary diet (carnivore, herbivore, omnivore), thermoregulation (ectotherm, endotherm) and locomotion mode (flying, running, swimming). As taxonomy and thermoregulation are highly correlated, we made a first model without taxonomy and a second model without thermoregulation and compared them by their Bayesian information criterion (BIC) values (see Methods for details). According to this, the model including thermoregulation instead of taxonomy is the most adequate ($\Delta\text{BIC}=27.37$). In this model, the differences between the diet types were not significant. In contrast, combinations of locomotion mode with thermoregulation exhibited significant differences (Fig. 3). In flying and running animals, endotherms generally tend to be faster than ectotherms (Fig. 3a,b). Metabolic constraints may enable endotherms to have higher activity levels than ectotherms at the low to intermediate temperatures most commonly encountered

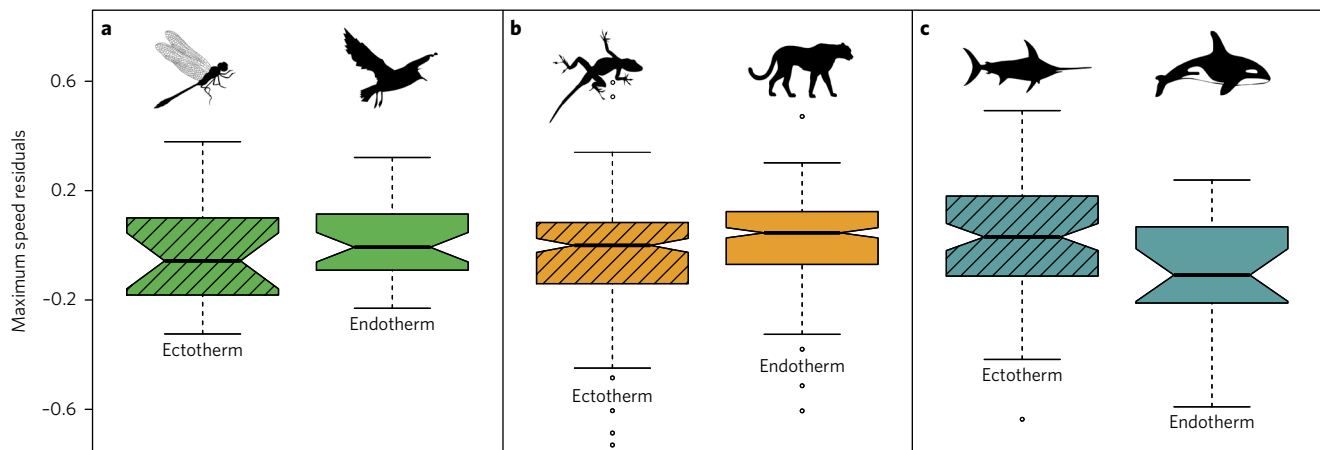


Figure 3 | Effect of thermoregulation on the maximum speed of animals. These are the residuals of the relationship in Fig. 2. **a, b**, In flying (**a**) and running (**b**) animals, endotherms are generally faster than ectotherms. **c**, In swimming animals, this effect is reversed, with ectotherms being generally faster than endotherms. Box plots show medians (horizontal line), an approximation of 95% confidence intervals suitable for comparing two medians (notches), 25th and 75th percentiles (boxes), the most extreme values (whiskers), and outliers (dots).

in nature³¹. This pattern is reversed in aquatic systems, in which endotherms (mammals and penguins) are significantly slower than ectotherms (mainly fish, Fig. 3c). We assume that this is due to the transition undergone by aquatic endotherms from a terrestrial to an aquatic lifestyle. Semi-aquatic endotherms are adapted to movement in two different media, which reduces swimming efficiency in comparison to wholly marine mammals: they have 2.4×10^5 times higher costs of transport³². But also, in marine mammals, costs of transport are considerably higher than in fish of similar size because they have higher energy expenditures for maintaining their body temperature³². Thus, the effect of thermoregulation on the allometric scaling of maximum speed depends on the locomotion mode and the medium. Future research combining maximum speed and ambient temperature data could provide a more detailed analysis of temperature effects on maximum speed. Overall, the significant effect of thermoregulation explained only ~4% of the residual variation, suggesting that the vast majority of the variation in speed across locomotion modes, ecosystem types and taxonomic groups is well explained by our maximum-speed model.

Discussion

Our findings help to solve one of the most challenging questions in movement ecology over recent decades: why are the largest animals not the fastest? Some studies have suggested a threshold beyond which animals run more slowly than predicted by a power-law relationship owing to biomechanical constraints¹³, thus implying that speed scaling depends on body-mass range^{11,12}. Others have invoked morphology, locomotion energetics and biomechanics^{10–13,15,17,18} to suggest that the maximum speed of running animals is constrained by the ability of muscles and bones to withstand the stress of the locomotor force hitting the ground^{17,18,33}. Size-related increases in locomotor stress may thus be mitigated by taxon-specific adaptations of bones, muscles and postures until eventually reaching limits at which larger body sizes come at the cost of reduced speed¹⁷. As these biomechanical concepts were lacking mechanistic predictions, the hump-shaped relationship between maximum speed and body mass has often been characterized with polynomial functions including linear and quadratic terms. We have thus also used polynomials as the best available alternative to compare against our model predictions. Although they offer a flexible way to describe nonlinear patterns, we find that polynomials do not predict the overall scaling relationship as accurately as our general time-dependent maximum-speed model, which

provides the single most general capture of patterns and processes across taxa and a larger body-mass range. Our speed predictions are thereby derived from only two main species traits: body mass and locomotion mode, which explain almost 90% ($R^2 = 0.893$) of the variation in maximum speed. This general approach allows a species-level prediction of speed which is crucial for understanding movement patterns, species interactions and animal space use.

However, our model allows prediction of the speed not only of extant but also of extinct species. For example, palaeontologists have long debated the potential running speeds of large birds³⁴ and dinosaurs^{35,36} that roamed past ecosystems. The benchmark of speed predictions is set by detailed morphological models^{35,36}. Interestingly, our maximum-speed model yields similar predictions by only accounting for body mass and locomotion mode (almost 80% of the morphological speed predictions are within the confidence intervals of our model predictions; Table 1). For instance, in contrast to a power-law model, the morphological and the time-dependent model predict lower speeds for *Tyrannosaurus* compared with the much smaller *Velociraptor*. This is consistent with theories claiming that *Tyrannosaurus* was very likely to have been a slow runner³⁷. A simple power-law model only yields reasonable results for lower body masses (such as flightless birds), whereas predictions for large species such as giant quadrupedal dinosaurs are unrealistically high. In contrast, our time-dependent model makes adequate predictions for small as well as large species including extinct dinosaurs (Fig. 4, green triangles). Note that the highly accurate prediction of the dinosaur speeds is achieved without free parameters as the model parameters are only obtained by fits to data of extant species (Fig. 2, and grey points in Fig. 4).

Our model also allows inferences to be drawn about evolutionary and ecological processes by analysing the deviations of empirically measured speeds from the model predictions. Higher maximum speeds than predicted indicate evolutionary pressure on optimizing speed capacities that could, for instance, arise from coevolution of pursuit predators and their prey.

Because many physiological and ecological processes such as metabolism, growth and feeding rates depend on ambient temperature (ectotherms) or body temperature (endotherms)^{38,39}, it is not surprising that some variables of movement speed and acceleration also increase with temperature⁴⁰. In our model, such a temperature dependence could be included as a Boltzmann factor in the constant a (equation (5)). Sufficient ambient temperature measurements at the point in time and space of the animals' maximum

Table 1 | Maximum-speed predictions for extant and extinct flightless birds, and bipedal and quadrupedal dinosaurs

Taxa	Body mass (kg)	Speed (km h ⁻¹)		
		Power law (95% CI)	Morphological models	Time-dependent model (95% CI)
Flightless birds				
<i>Dromaius</i> (extant)	27.2	40.92 (38.58–43.40)	47.88	57.62 (47.65–60.91)
<i>Struthio</i> (extant)	65.3	49.33 (46.27–52.59)	55.44	62.75 (46.71–66.03)
<i>Patagornis</i> (extinct)	45	45.56 (42.83–48.46)	50.40	61.34 (47.39–64.68)
Bipedal dinosaurs				
<i>Velociraptor</i>	20	38.32 (36.19–40.58)	38.88	54.56 (46.89–57.82)
<i>Allosaurus</i>	1,400	94.87 (87.09–103.34)	33.84	40.78 (28.93–44.83)
<i>Tyrannosaurus</i>	6,000	129.41 (117.47–142.57)	28.8	27.05 (17.84–31.52)
Quadrupedal dinosaurs				
<i>Triceratops</i>	8,478	139.32 (126.11–153.91)	26.4	24.36 (15.70–28.83)
<i>Apatosaurus</i>	27,869	179.59 (161.01–200.31)	12.3	16.75 (9.77–21.09)
<i>Brachiosaurus</i>	78,258	223.85 (199.00–251.80)	17.6	11.99 (6.39–16.04)

Model predictions of a simple power law, morphological models and our time-dependent maximum-speed model are compared (references in Supplementary Table 5). Confidence intervals (95% CI) are given for the power law and time-dependent model.

speed are currently lacking, but our model offers a framework to include temperature effects formally in future work.

In ecological research, our maximum-speed model provides a mechanistic understanding of the upper limit to animal movement patterns during migration, dispersal or bridging habitat patches. The travelling speed characterizing these movements is the fraction of maximum speed that can be maintained over longer periods of time. It would be interesting to analyse how travel speed scales with body mass on the large body-mass scale and whether it also follows a hump-shaped pattern. If so, animals would use an approximately fixed percentage of their maximum speed during travel. If, however, travel speed follows

a power-law relationship with body mass, large and small animals would use a higher proportion of their maximum speed during travel than intermediately sized animals. This would also affect different measurements of animal space use as well as migration and dispersal distances. Although home ranges⁴¹ and day ranges⁴² of animals have been shown to follow power-law relationships with body mass, migration distances of flying animals, for example, follow a curvilinear relationship with body mass⁴³. Our new results call for mechanistic analyses of how the hump-shaped scaling pattern of maximum speed could potentially affect other movement parameters.

The integration of our model as a species-specific scale (“what is physiologically possible”) with research on how this fraction is modified by species traits and environmental parameters such as landscape structure, resource availability and temperature (“what is ecologically realized in nature”) could help to provide a mechanistic understanding unifying physiological and ecological constraints on animal movement. In addition to generalizing our understanding across species traits and current landscape characteristics, this integrated approach will aid the prediction of how species-specific movement, and subsequently home ranges and meta-communities, may respond to ongoing landscape fragmentation and environmental change. Thus, our approach may act as a simple and powerful tool for predicting the natural boundaries of animal movement and help in gaining a more unified understanding of the currently assessed movement data across taxa and ecosystems^{6,7}.

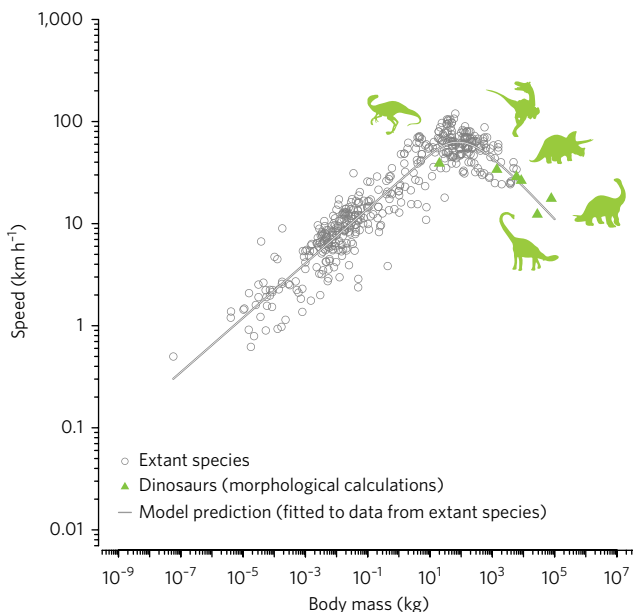


Figure 4 | Predicting the maximum speed of extinct species with the time-dependent model. The model prediction (grey line) is fitted to data of extant species (grey circles) and extended to higher body masses. Speed data for dinosaurs (green triangles) come from detailed morphological model calculations (values in Table 1) and were not used to obtain model parameters.

Methods

Data. We searched for published literature providing data on the maximum speeds of running, flying and swimming animals by using the search terms “maximum speed”, “escape speed” and “sprint speed”. From this list, we excluded publications on (1) vertical speeds (mainly published for birds) to avoid side-effects of gravitational acceleration that are not included in our model, or (2) the maxima of normal speeds (including also dispersal and migration). This resulted in a data set containing 622 data points for 474 species (see Supplementary Table 1 for an overview). Our data include laboratory and field studies as well as meta-studies (which are mainly field studies but may also include a minor amount of laboratory studies). For some data points, the study type could not be ascertained, and they were marked as “unclear”. For an overview of the study type of our data, see Supplementary Table 2.

Model fitting. We fitted several models to these data: (1) the time-dependent maximum-speed model (equation (5)), (2) three polynomial models (simple

polynomial model without cofactor; polynomial model with taxon as cofactor but without interaction term; and polynomial model with taxon as cofactor with interaction term) with linear and quadratic terms, and (3) three power-law models (simple power law without cofactor; power law with taxon as cofactor but without interaction term; and power law with taxon as cofactor with interaction term). For swimming animals, we excluded reptiles and arthropods from the statistical analyses as they contained only one data point each (see Supplementary Table 1). The polynomial and power-law models were fitted by the lm function, and the time-dependent model by the nls function in R (version 3.2.3)⁴⁴. The quality of the fits was compared according to the Bayesian information criterion (BIC) that combines the maximized value of the likelihood function with a penalty term for the number of parameters in the model. The model with the lowest BIC is preferred, and the results of this showed that the time-dependent maximum-speed model developed in the main text provided the best fit in all cases (see Supplementary Table 3). For flying animals, the simple polynomial model performed second best, whereas for running animals the polynomial model with taxon as cofactor with interaction term and for swimming animals the power-law model with taxon as cofactor with interaction term were second best (see Supplementary Table 3). Overall, the lower BIC values indicate that the time-dependent maximum-speed model provides a fit to the data that is substantially superior to power-law relationships, models with taxonomy as cofactor or (non-mechanistic but also hump-shaped) polynomials. The fitted parameter values of the time-dependent maximum-speed model for flying, running and swimming animals are given in Supplementary Table 4.

Residual variation analysis. We analysed the residuals of the time-dependent maximum-speed model (Fig. 2 of the main text) with respect to taxonomy (arthropods, birds, fish, mammals, molluscs, reptiles), primary diet type (carnivore, herbivore, omnivore), locomotion mode (flying, running, swimming) and thermoregulation (ectotherm, endotherm) using linear models. As taxonomy and thermoregulation are highly correlated, we made a first model without taxonomy and a second model without thermoregulation:

Model 1: residuals ~ (thermoregulation + diet type) × locomotion mode

Model 2: residuals ~ (taxonomy + diet type) × locomotion mode

We compared the two models by means of BIC and carried out a further mixed-effects model analysis on the superior model. This model included the study type as a random factor influencing the intercept, which ensures that differences among study types do not drive our statistical results. We acknowledge that the direct inclusion of multiple covariates in the model-fitting process would be preferable to residual analysis to avoid biased parameter estimates⁴⁵. However, this was impeded by the complexity of fitting the nonlinear model with four free parameters (equation (5)), and our main goal was less to estimate the exact parameters than to document the main variables affecting the unexplained variation.

Data availability. The data supporting the findings of this study are available within the Article and its Supplementary Information files.

Received: 8 November 2016; Accepted: 16 June 2017;
Published online: 17 July 2017

References

1. Jetz, W., Carbone, C., Fulford, J. & Brown, J. H. The scaling of animal space use. *Science* **306**, 266–268 (2004).
2. Bauer, S. & Hoyer, B. J. Migratory animals couple biodiversity and ecosystem functioning worldwide. *Science* **344**, 1242552 (2014).
3. Parmesan, C. & Yohe, G. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**, 37–42 (2003).
4. Pawar, S., Dell, A. I. & Savage, V. M. Dimensionality of consumer search space drives trophic interaction strengths. *Nature* **486**, 485–489 (2012).
5. Neutel, A.-M. et al. Reconciling complexity with stability in naturally assembling food webs. *Nature* **449**, 599–602 (2007).
6. Kays, R., Crofoot, M. C., Jetz, W. & Wikelski, M. Terrestrial animal tracking as an eye on life and planet. *Science* **348**, aaa2478 (2015).
7. Hussey, N. E. et al. Aquatic animal telemetry: a panoramic window into the underwater world. *Science* **348**, 1255642 (2015).
8. Peters, R. H. *The Ecological Implications of Body Size* (Cambridge Univ. Press, 1983).
9. Hedenström, A. Scaling migration speed in animals that run, swim and fly. *J. Zool.* **259**, 155–160 (2003).
10. Bejan, A. & Marden, J. H. Unifying constructal theory for scale effects in running, swimming and flying. *J. Exp. Biol.* **209**, 238–248 (2006).
11. Iriarte-Díaz, J. Differential scaling of locomotor performance in small and large terrestrial mammals. *J. Exp. Biol.* **205**, 2897–2908 (2002).
12. Fuentes, M. A. Theoretical considerations on maximum running speeds for large and small animals. *J. Theor. Biol.* **390**, 127–135 (2016).

13. Garland, T. The relation between maximal running speed and body mass in terrestrial mammals. *J. Zool.* **199**, 157–170 (1983).
14. Clemente, C. J. & Richards, C. Muscle function and hydrodynamics limit power and speed in swimming frogs. *Nat. Commun.* **4**, 2737 (2013).
15. Clemente, C. J., Thompson, G. G. & Withers, P. C. Evolutionary relationships of sprint speed in Australian varanid lizards. *J. Zool.* **278**, 270–280 (2009).
16. Van Damme, R. & Vanhooydonck, B. Origins of interspecific variation in lizard sprint capacity. *Funct. Ecol.* **15**, 186–202 (2001).
17. Dick, T. J. & Clemente, C. J. Where have all the giants gone? How animals deal with the problem of size. *PLoS Biol.* **15**, e2000473 (2017).
18. Clemente, C. J., Withers, P. C. & Thompson, G. Optimal body size with respect to maximal speed for the yellow-spotted monitor lizard (*Varanus panoptes*; Varanidae). *Physiol. Biochem. Zool.* **85**, 265–273 (2012).
19. Alexander, R. M. *Principles of Animal Locomotion* (Princeton Univ. Press, 2003).
20. Huey, R. B. & Hertz, P. E. Effects of body size and slope on acceleration of a lizard (*Stellio stellio*). *J. Exp. Biol.* **110**, 113–123 (1984).
21. Elliott, J. P., Cowan, I. M. & Holling, C. S. Prey capture by the African lion. *Can. J. Zool.* **55**, 1811–1828 (1977).
22. Garcia, G. J. & da Silva, J. K. On the scaling of mammalian long bones. *J. Exp. Biol.* **207**, 1577–1584 (2004).
23. Biewener, A. A. Biomechanical consequences of scaling. *J. Exp. Biol.* **208**, 1665–1676 (2005).
24. Jones, J. H. & Lindstedt, S. L. Limits to maximal performance. *Annu. Rev. Physiol.* **55**, 547–569 (1993).
25. Weyand, P. G. & Bundle, M. W. Energetics of high-speed running: integrating classical theory and contemporary observations. *Am. J. Physiol. Regul. Integr. Comp. Physiol.* **288**, R956–R965 (2005).
26. Pollock, C. M. & Shadwick, R. E. Allometry of muscle, tendon, and elastic energy storage capacity in mammals. *Am. J. Physiol. Regul. Integr. Comp. Physiol.* **266**, R1022–R1031 (1994).
27. Alexander, R. M., Jayes, A. S., Maloiy, G. M. O. & Wathuta, E. M. Allometry of the leg muscles of mammals. *J. Zool.* **194**, 539–552 (1981).
28. Bennett, M. B. Allometry of the leg muscles of birds. *J. Zool.* **238**, 435–443 (1996).
29. Maloiy, G. M. O., Alexander, R., Njau, R. & Jayes, A. S. Allometry of the legs of running birds. *J. Zool.* **187**, 161–167 (1979).
30. *Comparative Physiology: Life in Water and on Land* (eds Dejours, P. et al.) (FIDIA Research Series Vol. 9, Springer, 1987).
31. Gillooly, J. F., Brown, J. H., West, G. B., Savage, V. M. & Charnov, E. L. Effects of size and temperature on metabolic rate. *Science* **293**, 2248–2251 (2001).
32. Williams, T. M. The evolution of cost efficient swimming in marine mammals: limits to energetic optimization. *Phil. Trans. R. Soc. Lond. B Biol. Sci.* **354**, 193–201 (1999).
33. Biewener, A. A. Bone strength in small mammals and bipedal birds: do safety factors change with body size? *J. Exp. Biol.* **98**, 289–301 (1982).
34. Blanco, R. E. & Jones, W. W. Terror birds on the run: a mechanical model to estimate its maximum running speed. *Proc. R. Soc. B Biol. Sci.* **272**, 1769–1773 (2005).
35. Thulborn, R. A. Speeds and gaits of dinosaurs. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **38**, 227–256 (1982).
36. Sellers, W. I. & Manning, P. L. Estimating dinosaur maximum running speeds using evolutionary robotics. *Proc. R. Soc. Lond. B Biol. Sci.* **274**, 2711–2716 (2007).
37. Hutchinson, J. R. & Garcia, M. Tyrannosaurus was not a fast runner. *Nature* **415**, 1018–1021 (2002).
38. Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M. & West, G. B. Toward a metabolic theory of ecology. *Ecology* **85**, 1771–1789 (2004).
39. Rall, B. C. et al. Universal temperature and body-mass scaling of feeding rates. *Phil. Trans. R. Soc. Lond. B Biol. Sci.* **367**, 2923–2934 (2012).
40. Dell, A. I., Pawar, S. & Savage, V. M. Systematic variation in the temperature dependence of physiological and ecological traits. *Proc. Natl Acad. Sci. USA* **108**, 10591–10596 (2011).
41. Tamburello, N., Côté, I. M. & Dulvy, N. K. Energy and the scaling of animal space use. *Am. Nat.* **186**, 196–211 (2015).
42. Carbone, C., Cowlshaw, G., Isaac, N. J. B. & Rowcliffe, J. M. How far do animals go? Determinants of day range in mammals. *Am. Nat.* **165**, 290–297 (2005).
43. Hein, A. M., Hou, C. & Gillooly, J. F. Energetic and biomechanical constraints on animal migration distance. *Ecol. Lett.* **15**, 104–110 (2012).
44. R Core Team. *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, 2015).
45. Freckleton, R. P. On the misuse of residuals in ecology: regression of residuals vs. multiple regression. *J. Anim. Ecol.* **71**, 542–545 (2002).

Acknowledgements

M.R.H., W.J., B.C.R. and U.B. acknowledge the support of the German Centre for integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig funded by the German Research Foundation (FZT 118).

Author contributions

M.R.H. and U.B. developed the model. M.R.H. gathered the data. M.R.H. and B.C.R. carried out statistical analyses. W.J. was involved in study concept and data analyses. M.R.H. and U.B. wrote the paper. All authors discussed the results and commented on the manuscript.

Competing interests

The authors declare no competing financial interests.

Additional information

Supplementary information is available for this paper at doi:10.1038/s41559-017-0241-4.

Reprints and permissions information is available at www.nature.com/reprints.

Correspondence and requests for materials should be addressed to U.B.

Publisher's note: Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

In the format provided by the authors and unedited.

A general scaling law reveals why the largest animals are not the fastest

Myriam R. Hirt^{1,2*}, Walter Jetz^{1,3,4}, Björn C. Rall^{1,2} and Ulrich Brose^{1,2}

¹EcoNetLab, German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig 04103, Germany. ²EcoNetLab, Friedrich Schiller University Jena, Dornburger Strasse 159, 07743 Jena, Germany. ³Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT 06511, USA.

⁴Department of Life Sciences, Imperial College London, Silwood Park, Ascot SL5 7QN, UK. *e-mail: myriam.hirt@idiv.de

Supplementary Information for

A general scaling law reveals why the largest animals are not the fastest

Myriam R. Hirt, Walter Jetz, Björn C. Rall, Ulrich Brose

Supplementary Table 1

Distribution of data across movement types and taxa.

movement mode	taxonomic group	n data points
running	arthropods	50
	birds	3
	mammals	261
	reptiles	144
flying	arthropods	19
	birds	29
	mammals	7
swimming	arthropods	1
	birds	5
	fish	81
	mammals	16
	mollusks	5
	reptiles	1

Supplementary Table 2

Distribution of data across study and publication types.

study type	nbr. of data points
field study	33
laboratory study	119
meta-study	404
unclear	66

Supplementary Table 3

Δ BIC values for comparing the seven speed models. Taxonomic groups comprise arthropods, birds, fish, mammals, mollusks, reptiles.

Models	flying	Δ BIC running	swimming
time-dependent model	0	0	0
Polynomial	6.79	118.20	19.51
polynomial (* taxon)	17.96	15.97	24.90
polynomial (+ taxon)	8.03	78.60	18.81
power law (* taxon)	12.90	122.57	8.82
power law (+ taxon)	13.52	112.38	25.55
power law	11.95	191.66	46.48

Note that for the time-dependent model, taxon could not be directly included because of the complexity of fitting a non-linear model with four free parameters. Therefore, we conducted a residual analysis (see main text).

Supplementary Table 4

Fitted values of the time-dependent maximum speed model: parameters a , b , h and i (from Eq. 5) with standard errors and resulting equations for the different movement modes (flying, running, swimming). Body mass M in kg and speed v in km h^{-1} .

movement mode	a	b	h	i	equation
flying	142.8 ± 16.7	0.24 ± 0.01	2.4 ± 1.4	-0.72 ± 0.26	$v_{real} = 142.8 M^{0.24}(1 - e^{-2.4 M^{-0.72}})$
running	25.5 ± 0.84	0.26 ± 0.006	22 ± 7.6	-0.6 ± 0.05	$v_{real} = 25.5 M^{0.26}(1 - e^{-22 M^{-0.6}})$
swimming	11.2 ± 0.91	0.36 ± 0.02	19.5 ± 13.6	-0.56 ± 0.07	$v_{real} = 11.2 M^{0.36}(1 - e^{-19.5 M^{-0.56}})$

Supplementary Table 5

References for the masses and speed predictions of Table 1 in the main text.

species	mass	power law	reference	
			morphological model	time-dependent model
<i>Dromaius</i>	(1)	*	(1)	+
<i>Struthio</i>	(1)	*	(1)	+
<i>Patagornis</i>	(2)	*	(2)	+
<i>Velociraptor</i>	(1)	*	(1)	+
<i>Allosaurus</i>	(1)	*	(1)	+
<i>Tyrannosaurus</i>	(1)	*	(1)	+
<i>Triceratops</i>	(3)	*	(3)	+
<i>Apatosaurus</i>	(3)	*	(3)	+
<i>Brachiosaurus</i>	(3)	*	(3)	+

* prediction from a power law (equ. 1)

+ prediction from our model (equ. 5)

References

1. Blanco, R. E. & Jones, W. W. Terror birds on the run: a mechanical model to estimate its maximum running speed. *Proc. R. Soc. B Biol. Sci.* **272**, 1769–1773 (2005).
2. Sellers, W. I. & Manning, P. L. Estimating dinosaur maximum running speeds using evolutionary robotics. *Proc. R. Soc. Lond. B Biol. Sci.* **274**, 2711–2716 (2007).
3. Thulborn, R. A. Speeds and gaits of dinosaurs. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **38**, 227–256 (1982).

Maximum speed data base

species	taxonomic group	locomotion mode	thermoregulation	body mass [kg]	mass ref.	max. speed [km/h]	speed ref.	primary diet
<i>Aeshna cyanea</i>	arthropod	flying	ectotherm	4.22E-04	28	36	70	carnivore
<i>Anax junius</i>	arthropod	flying	ectotherm	4.50E-04	28	27	70	carnivore
<i>Anax parthenope julius</i>	arthropod	flying	ectotherm	3.90E-04	28	25.92	4	carnivore
<i>Anax sp.</i>	arthropod	flying	ectotherm	0.0138	11	36	11	carnivore
<i>Anopheles ziemanni</i>	arthropod	flying	ectotherm	5.22E-06	92	6.48	36	carnivore
<i>Anthonomus grandis</i>	arthropod	flying	ectotherm	6.86E-06	94	4.8	55	herbivore
<i>Culex pipiens</i>	arthropod	flying	ectotherm	1.30E-06	51	3.6	19	carnivore
<i>Drosophila hydei</i>	arthropod	flying	ectotherm	1.76E-07	64	3.24	25	herbivore
<i>Drosophila melanogaster</i>	arthropod	flying	ectotherm	7.47E-07	11	6.84	11	herbivore
<i>Drosophila melanogaster</i>	arthropod	flying	ectotherm	7.89E-08	64	3.06	52	herbivore
<i>Drosophila virilis</i>	arthropod	flying	ectotherm	2.05E-07	64	4.32	81	herbivore
<i>Eristalis sp.</i>	arthropod	flying	ectotherm	9.00E-05	37	36	20	herbivore
<i>Volucella pellucens</i>	arthropod	flying	ectotherm	1.70E-04	37	36	20	herbivore
<i>Euglossa imperialis</i>	arthropod	flying	ectotherm	0.0015	29	25.56	21	herbivore
<i>Leptocoris chinensis</i>	arthropod	flying	ectotherm	4.73E-05	42	6	77	herbivore
<i>Manduca sexta</i>	arthropod	flying	ectotherm	0.002	29	19.08	75	herbivore
<i>Manduca sexta</i>	arthropod	flying	ectotherm	0.002	29	18	86	herbivore
<i>Riptortus pedestris</i>	arthropod	flying	ectotherm	6.52E-05	47	10.8	77	herbivore
<i>Tabanus affinis</i>	arthropod	flying	ectotherm	1.01E-04	11	23.76	11	carnivore
<i>Accipiter striatus</i>	bird	flying	endotherm	0.0965	30	64	12	carnivore
<i>Anas acuta</i>	bird	flying	endotherm	0.947	30	82.08	11	omnivore
<i>Anas platyrhynchos</i>	bird	flying	endotherm	1.14	30	105	101	omnivore
<i>Apus apus</i>	bird	flying	endotherm	0.058	11	91.8	11	carnivore
<i>Aquila chrysaetos</i>	bird	flying	endotherm	4.2635	30	129	93	carnivore
<i>Archilochus colubris</i>	bird	flying	endotherm	0.0075	11	40.32	11	herbivore
<i>Buteo jamaicensis</i>	bird	flying	endotherm	1.11	30	195	101	carnivore
<i>Calypte anna</i>	bird	flying	endotherm	0.0044	56	56.16	17	herbivore
<i>Chen caerulescens</i>	bird	flying	endotherm	2.641	30	185	46	herbivore

<i>Columba livia</i>	bird	flying	endotherm	0.3545	30	136.8	101	herbivore
<i>Cygnus columbianus</i>	bird	flying	endotherm	6.75	30	135	31	omnivore
<i>Cygnus columbianus bewickii</i>	bird	flying	endotherm	6.05	11	67.68	11	omnivore
<i>Cygnus cygnus</i>	bird	flying	endotherm	9.35	30	88	39	omnivore
<i>Diomedea exulans</i>	bird	flying	endotherm	8.19	30	127	71	carnivore
<i>Falco peregrinus</i>	bird	flying	endotherm	0.78	30	110	96	carnivore
<i>Fregata aquila</i>	bird	flying	endotherm	1.5	101	153	101	carnivore
<i>Gymnogyps californianus</i>	bird	flying	endotherm	4.49	30	90	101	carnivore
<i>Hirundapus caudacutus</i>	bird	flying	endotherm	0.096	30	170	101	carnivore
<i>Mergus serrator</i>	bird	flying	endotherm	1.02	30	129	101	carnivore
<i>Morus bassanus</i>	bird	flying	endotherm	3	30	100	101	carnivore
<i>Numenius phaeopus</i>	bird	flying	endotherm	0.366	30	83.52	11	carnivore
<i>Nymphicus hollandicus</i>	bird	flying	endotherm	0.088	30	46.8	41	herbivore
<i>Otis tarda</i>	bird	flying	endotherm	10.55	30	80	43	herbivore
<i>Pelecanus onocrotalus</i>	bird	flying	endotherm	9.52	30	82.08	11	carnivore
<i>Phylloscopus trochilus</i>	bird	flying	endotherm	0.0087	30	43.2	11	carnivore
<i>Plectropterus gambensis</i>	bird	flying	endotherm	3.869	30	142	101	omnivore
<i>Somateria mollissima</i>	bird	flying	endotherm	2.07	30	113	101	carnivore
<i>Thalassarche chrysostoma</i>	bird	flying	endotherm	3.51	30	127	14	carnivore
<i>Xanthocephalus xanthocephalus</i>	bird	flying	endotherm	0.0646	30	56.33	23	omnivore
<i>Chalinolobus tuberculatus</i>	mammal	flying	endotherm	0.0085	60	60	60	carnivore
<i>Euderma maculatum</i>	mammal	flying	endotherm	0.0162	56	53	15	carnivore
<i>Glossophaga soricina</i>	mammal	flying	endotherm	0.0103	56	37.8	88	herbivore
<i>Lasiurus borealis</i>	mammal	flying	endotherm	0.013	56	64	62	carnivore
<i>Lasiurus semotus</i>	mammal	flying	endotherm	0.02603	56	54.72	62	carnivore
<i>Nyctinomops macrotis</i>	mammal	flying	endotherm	0.023	56	61	22	carnivore
<i>Tadarida brasiliensis</i>	mammal	flying	endotherm	0.0125	56	96.5	26	carnivore
<i>Agelenopsis aperta</i>	arthropod	running	ectotherm	1.28E-04	3	0.933	66	carnivore
<i>Argiope keyserlingi</i>	arthropod	running	ectotherm	4.02E-06	65	1.2	65	carnivore
<i>Blaberus discoidalis</i>	arthropod	running	ectotherm	0.003	76	1.998	76	omnivore
<i>Carabinae</i>	arthropod	running	ectotherm	8.68E-05	32	2.14	32	carnivore
<i>Carabinae</i>	arthropod	running	ectotherm	8.85E-05	32	2.24	32	carnivore
<i>Carabinae</i>	arthropod	running	ectotherm	7.28E-05	32	2.25	32	carnivore

<i>Carabinae</i>	arthropod	running	ectotherm	1.40E-04	32	2.27	32	carnivore
<i>Cataglyphis sp.</i>	arthropod	running	ectotherm	1.55E-05	83	2.088	40	carnivore
<i>Cicindela eburneola</i>	arthropod	running	ectotherm	3.89E-05	45	6.696	45	carnivore
<i>Cicindela hudsoni</i>	arthropod	running	ectotherm	2.00E-04	45	9	45	carnivore
<i>Cicindela leucothrix</i>	arthropod	running	ectotherm	6.20E-05	45	3.67	45	carnivore
<i>Cicindela repanda</i>	arthropod	running	ectotherm	4.76E-05	87	1.91	35	carnivore
<i>Cicindela saetigera</i>	arthropod	running	ectotherm	7.08E-05	45	5.04	45	carnivore
<i>Cicindela salicursoria</i>	arthropod	running	ectotherm	4.36E-05	45	5.29	45	carnivore
<i>Cicindela velox</i>	arthropod	running	ectotherm	8.60E-05	45	6.95	45	carnivore
<i>Dolomedes fimbriatus</i>	arthropod	running	ectotherm	1.87E-04	9	0.976	9	carnivore
<i>Dolomedes plantarius</i>	arthropod	running	ectotherm	1.79E-04	67	2.7	38	carnivore
<i>Dolomedes triton</i>	arthropod	running	ectotherm	4.00E-04	9	1.14	9	carnivore
<i>Hogna carolinensis (female)</i>	arthropod	running	ectotherm	1.26E-04	57	4.50	57	carnivore
<i>Hogna carolinensis (male)</i>	arthropod	running	ectotherm	1.02E-04	57	4.73	57	carnivore
<i>Hololena adnexa</i>	arthropod	running	ectotherm	2.64E-05	74	2.16	74	carnivore
<i>Hololena curta</i>	arthropod	running	ectotherm	2.64E-05	74	1.83	74	carnivore
<i>insect</i>	arthropod	running	ectotherm	0.001	7	3.6	7	herbivore
<i>insect</i>	arthropod	running	ectotherm	0.001	7	5.4	7	herbivore
<i>insect</i>	arthropod	running	ectotherm	0.05	7	2.88	7	herbivore
<i>Ocymyrmex barbiger</i>	arthropod	running	ectotherm	4.10E-06	53	1.38	53	omnivore
<i>Paratarsotomus macropalpis</i>	arthropod	running	ectotherm	1.82E-07	89	0.5	89	carnivore
<i>Paratarsotomus macropalpis</i>	arthropod	running	ectotherm	2.68E-07	69	0.63	69	carnivore
<i>Parateneriffia spp.</i>	arthropod	running	ectotherm	3.00E-08	89	0.4716	89	carnivore
<i>Pardosa amentata</i>	arthropod	running	ectotherm	1.10E-05	67	1.476	24	carnivore
<i>Pardosa lugubris</i>	arthropod	running	ectotherm	1.03E-05	67	1.44	13	carnivore
<i>Pardosa valens</i>	arthropod	running	ectotherm	8.50E-05	1	1.53	1	carnivore
<i>Periplaneta americana</i>	arthropod	running	ectotherm	8.30E-04	33	5.4	33	omnivore
<i>Pirata sedentarius (Size class 1)</i>	arthropod	running	ectotherm	1.52E-05	2	0.915	2	carnivore
<i>Pirata sedentarius (Size class 2)</i>	arthropod	running	ectotherm	2.25E-05	2	0.791	2	carnivore
<i>Pirata sedentarius (Size class 3)</i>	arthropod	running	ectotherm	3.62E-05	2	1.22	2	carnivore
<i>Pirata sedentarius (Size class 4)</i>	arthropod	running	ectotherm	5.85E-05	2	1.57	2	carnivore
<i>Schizocosa ocreata (Size class 1)</i>	arthropod	running	ectotherm	1.78E-05	24	0.621	24	carnivore
<i>Schizocosa ocreata (Size class 2)</i>	arthropod	running	ectotherm	2.56E-05	24	1.60	24	carnivore

<i>Schizocosa ocreata</i> (Size class 3)	arthropod	running	ectotherm	3.11E-05	24	2.53	24	carnivore
<i>Schizocosa ocreata</i> (Size class 4)	arthropod	running	ectotherm	4.49E-05	24	2.64	24	carnivore
<i>Schizocosa ocreata</i> (Size class 5)	arthropod	running	ectotherm	5.30E-05	24	2.23	24	carnivore
<i>Servaea incana</i>	arthropod	running	ectotherm	5.36E-05	54	0.9	54	carnivore
<i>Varacosa terricola</i> (Size class 1)	arthropod	running	ectotherm	1.76E-04	24	2.57	24	carnivore
<i>Varacosa terricola</i> (Size class 2)	arthropod	running	ectotherm	2.87E-04	24	2.57	24	carnivore
<i>Varacosa terricola</i> (Size class 3)	arthropod	running	ectotherm	3.20E-04	24	2.50	24	carnivore
<i>Varacosa terricola</i> (Size class 4)	arthropod	running	ectotherm	4.87E-04	24	2.72	24	carnivore
<i>Varacosa terricola</i> (Size class 5)	arthropod	running	ectotherm	5.28E-04	24	2.24	24	carnivore
<i>Varacosa terricola</i> (Size class 6)	arthropod	running	ectotherm	6.01E-04	24	2.11	24	carnivore
<i>Varacosa terricola</i> (Size class 7)	arthropod	running	ectotherm	7.17E-04	24	1.84	24	carnivore
<i>Geococcyx californianus</i>	bird	running	endotherm	0.5	101	32	101	omnivore
<i>Struthio camelus</i>	bird	running	endotherm	111	30	70	101	herbivore
<i>Struthio camelus</i>	bird	running	endotherm	111	30	82.8	11	herbivore
<i>Acinonyx jubatus</i>	mammal	running	endotherm	39	16	104.95	16	carnivore
<i>Acinonyx jubatus</i>	mammal	running	endotherm	65	101	120	101	carnivore
<i>Acinonyx jubatus</i>	mammal	running	endotherm	58.8	44	106.91	44	carnivore
<i>Acinonyx jubatus</i>	mammal	running	endotherm	44.87	11	104.4	11	carnivore
<i>Aepyceros melampus</i>	mammal	running	endotherm	50	16	74.99	16	herbivore
<i>Aepyceros melampus</i>	mammal	running	endotherm	50	34	47	34	herbivore
<i>Aepyceros melampus</i>	mammal	running	endotherm	53.25	7	45.68	7	herbivore
<i>Alcelaphus buselaphus</i>	mammal	running	endotherm	150	16	69.98	16	herbivore
<i>Alcelaphus buselaphus</i>	mammal	running	endotherm	170	34	80	34	herbivore
<i>Alcelaphus buselaphus</i>	mammal	running	endotherm	136	7	77.98	7	herbivore
<i>Alces alces</i>	mammal	running	endotherm	410.2	16	55.98	16	herbivore
<i>Alces alces</i>	mammal	running	endotherm	384	7	54.55	7	herbivore
<i>Ammospermophilus leucurus</i>	mammal	running	endotherm	0.0759	44	16.77	44	omnivore
<i>Antechinomys laniger</i>	mammal	running	endotherm	0.025	44	14.51	44	carnivore
<i>Antechinus flavipes</i>	mammal	running	endotherm	0.052	44	16.20	44	carnivore
<i>Antechinus stuartii</i>	mammal	running	endotherm	0.0315	44	17.38	44	carnivore
<i>Antidorcas marsupialis</i>	mammal	running	endotherm	21.18	16	87.90	16	herbivore
<i>Antidorcas marsupialis</i>	mammal	running	endotherm	34	34	97	34	herbivore
<i>Antidorcas marsupialis</i>	mammal	running	endotherm	34	7	94.302	7	herbivore

<i>Antilocapra americana</i>	mammal	running	endotherm	46.03	16	87.10	16	herbivore
<i>Antilocapra americana</i>	mammal	running	endotherm	50	101	98	101	herbivore
<i>Antilope cervicapra</i>	mammal	running	endotherm	37	34	105	34	herbivore
<i>Antilope cervicapra</i>	mammal	running	endotherm	34.99	16	94.84	16	herbivore
<i>Antilope cervicapra</i>	mammal	running	endotherm	37.5	7	102.08	7	herbivore
<i>Axis axis</i>	mammal	running	endotherm	45.5	56	65	102	herbivore
<i>Bettongia penicillata</i>	mammal	running	endotherm	1.1	44	24.11	44	herbivore
<i>Bison bison</i>	mammal	running	endotherm	624.58	56	52.00	16	herbivore
<i>Bison bison</i>	mammal	running	endotherm	865	7	54.43	7	herbivore
<i>Bison bonasus</i>	mammal	running	endotherm	225	16	55.98	16	herbivore
<i>Bos sauveli</i>	mammal	running	endotherm	800	34	29	34	herbivore
<i>Bos sauveli</i>	mammal	running	endotherm	800	7	28.15	7	herbivore
<i>Boselaphus tragocamelus</i>	mammal	running	endotherm	200	16	47.97	16	herbivore
<i>Camelus bactrianus</i>	mammal	running	endotherm	549.54	16	59.98	16	herbivore
<i>Camelus dromedarius</i>	mammal	running	endotherm	500	34	32	34	herbivore
<i>Camelus dromedarius</i>	mammal	running	endotherm	414.95	16	52.00	16	herbivore
<i>Camelus dromedarius</i>	mammal	running	endotherm	550	7	31.09	7	herbivore
<i>Canis aureus</i>	mammal	running	endotherm	9.2	16	55.98	16	carnivore
<i>Canis aureus</i>	mammal	running	endotherm	8.8	44	54.44	44	carnivore
<i>Canis familiaris</i>	mammal	running	endotherm	17	34	54.95	16	carnivore
<i>Canis familiaris</i>	mammal	running	endotherm	25	44	65.14	44	carnivore
<i>Canis latrans</i>	mammal	running	endotherm	12.3	16	55.98	16	carnivore
<i>Canis latrans</i>	mammal	running	endotherm	18	101	69.04	101	carnivore
<i>Canis latrans</i>	mammal	running	endotherm	13.3	44	63.19	44	carnivore
<i>Canis lupus</i>	mammal	running	endotherm	40	34	63.97	16	carnivore
<i>Canis lupus</i>	mammal	running	endotherm	35.3	44	62.06	44	carnivore
<i>Canis mesomelas</i>	mammal	running	endotherm	7.6	16	59.98	16	carnivore
<i>Canis mesomelas</i>	mammal	running	endotherm	7	44	58.29	44	carnivore
<i>Capra aegaerus</i>	mammal	running	endotherm	46	16	44.98	16	herbivore
<i>Capra aegagrus</i>	mammal	running	endotherm	30	7	43.75	7	herbivore
<i>Capra aegagrus</i>	mammal	running	endotherm	30	7	78.09	7	herbivore
<i>Capra caucasica</i>	mammal	running	endotherm	55	16	44.98	16	herbivore
<i>Capreolus capreolus</i>	mammal	running	endotherm	25	16	59.98	16	herbivore

<i>Ceratotherium simum</i>	mammal	running	endotherm	2000	7	24.36	7	herbivore
<i>Ceratotherium simum</i>	mammal	running	endotherm	1901	16	39.99	16	herbivore
<i>Ceratotherium simum</i>	mammal	running	endotherm	3000	34	25	34	herbivore
<i>Cercartetus concinnus</i>	mammal	running	endotherm	0.015	44	4.84	44	carnivore
<i>Cervus canadensis</i>	mammal	running	endotherm	382	101	72.4	101	herbivore
<i>Cervus elaphus</i>	mammal	running	endotherm	84.92	16	71.94	16	herbivore
<i>Chaetodipus baileyi</i>	mammal	running	endotherm	0.0391	44	12.09	44	herbivore
<i>Chaetodipus fallax</i>	mammal	running	endotherm	0.018	44	12.45	44	herbivore
<i>Connochaetes gnou</i>	mammal	running	endotherm	157	16	79.98	16	herbivore
<i>Connochaetes gnou</i>	mammal	running	endotherm	250	101	64	101	herbivore
<i>Connochaetes gnou</i>	mammal	running	endotherm	300	34	90	34	herbivore
<i>Connochaetes gnou</i>	mammal	running	endotherm	132.25	56	62.18	7	herbivore
<i>Connochaetes gnou</i>	mammal	running	endotherm	132.25	56	69.97	7	herbivore
<i>Connochaetes taurinus</i>	mammal	running	endotherm	180	34	79.98	16	herbivore
<i>Crocota crocuta</i>	mammal	running	endotherm	65.01	16	59.98	16	carnivore
<i>Crocota crocuta</i>	mammal	running	endotherm	50	101	64	101	carnivore
<i>Crocota crocuta</i>	mammal	running	endotherm	52	44	62.99	44	carnivore
<i>Dama dama</i>	mammal	running	endotherm	45	16	65.01	16	herbivore
<i>Dama dama</i>	mammal	running	endotherm	55	7	63.40	7	herbivore
<i>Damaliscus dorcas</i>	mammal	running	endotherm	43.45	16	69.98	16	herbivore
<i>Damaliscus hunteri</i>	mammal	running	endotherm	158.85	16	69.98	16	herbivore
<i>Damaliscus lunatus</i>	mammal	running	endotherm	125.89	16	69.98	16	herbivore
<i>Damaliscus lunatus</i>	mammal	running	endotherm	130	7	68.24	7	herbivore
<i>Dasyuroides byrnei</i>	mammal	running	endotherm	0.12	44	25.66	44	carnivore
<i>Diceros bicornis</i>	mammal	running	endotherm	875	16	44.98	16	herbivore
<i>Diceros bicornis</i>	mammal	running	endotherm	1200	7	43.80	7	herbivore
<i>Dipodomys deserti</i>	mammal	running	endotherm	0.0976	44	14.63	44	herbivore
<i>Dipodomys merriami</i>	mammal	running	endotherm	0.035	44	31.22	44	herbivore
<i>Dipodomys microps</i>	mammal	running	endotherm	0.056	44	20.43	44	herbivore
<i>Dipodomys ordii</i>	mammal	running	endotherm	0.0478	44	13.66	44	herbivore
<i>Elephas maximus</i>	mammal	running	endotherm	4000	34	26	34	herbivore
<i>Elephas maximus</i>	mammal	running	endotherm	4000	7	25.28	7	herbivore
<i>Equus asinus</i>	mammal	running	endotherm	165.2	16	54.95	16	herbivore

<i>Equus burchelli</i>	mammal	running	endotherm	136.14	16	69.98	16	herbivore
<i>Equus burchelli</i>	mammal	running	endotherm	235	7	68.15	7	herbivore
<i>Equus caballus</i>	mammal	running	endotherm	529.66	16	63.97	16	herbivore
<i>Equus caballus</i>	mammal	running	endotherm	350	7	68.04	7	herbivore
<i>Equus caballus</i>	mammal	running	endotherm	600	101	88	101	herbivore
<i>Equus hemionus</i>	mammal	running	endotherm	220.8	16	63.97	16	herbivore
<i>Equus hemionus</i>	mammal	running	endotherm	220.8	16	63.97	16	herbivore
<i>Equus hemionus</i>	mammal	running	endotherm	230	101	64	101	herbivore
<i>Equus hemionus</i>	mammal	running	endotherm	200	7	68.04	7	herbivore
<i>Equus hemionus</i>	mammal	running	endotherm	200	7	68.04	7	herbivore
<i>Equus zebra</i>	mammal	running	endotherm	276.06	16	63.97	16	herbivore
<i>Equus zebra</i>	mammal	running	endotherm	328	101	64.4	101	herbivore
<i>Eudorcas thomsonii</i>	mammal	running	endotherm	20	101	65	101	herbivore
<i>Felis catus</i>	mammal	running	endotherm	6	101	48	101	carnivore
<i>Gazella dorcas</i>	mammal	running	endotherm	19	16	79.98	16	herbivore
<i>Gazella granti</i>	mammal	running	endotherm	50	16	80.91	16	herbivore
<i>Gazella subgutturosa</i>	mammal	running	endotherm	24	16	97.05	16	herbivore
<i>Gazella thomsoni</i>	mammal	running	endotherm	19	16	79.98	16	herbivore
<i>Giraffa camelopardalis</i>	mammal	running	endotherm	1700	16	55.98	16	herbivore
<i>Giraffa camelopardalis</i>	mammal	running	endotherm	1700	101	52	101	herbivore
<i>Giraffa camelopardalis</i>	mammal	running	endotherm	1000	34	60	34	herbivore
<i>Giraffa camelopardalis</i>	mammal	running	endotherm	1075	7	58.41	7	herbivore
<i>Gorilla gorilla</i>	mammal	running	endotherm	127	44	31.08	44	herbivore
<i>Heteromys desmarestianus</i>	mammal	running	endotherm	0.05	44	12.19	44	herbivore
<i>Hippopotamus amphibius</i>	mammal	running	endotherm	1210.60	16	25.00	16	herbivore
<i>Hippopotamus amphibius</i>	mammal	running	endotherm	3800	7	24.36	7	herbivore
<i>Hippotragus equinus</i>	mammal	running	endotherm	224.91	16	55.98	16	herbivore
<i>Hippotragus equinus</i>	mammal	running	endotherm	226.5	7	54.58	7	herbivore
<i>Hippotragus niger</i>	mammal	running	endotherm	181.13	16	57.02	16	herbivore
<i>Homo sapiens</i>	mammal	running	endotherm	70	44	38.83	44	omnivore
<i>Homo sapiens</i>	mammal	running	endotherm	70	7	43.85	7	omnivore
<i>Hyaena hyaena</i>	mammal	running	endotherm	31.99	16	50.00	16	carnivore
<i>Hyaena hyaena</i>	mammal	running	endotherm	26.8	44	48.47	44	carnivore

<i>Isoodon obesulus</i>	mammal	running	endotherm	0.718	44	13.90	44	omnivore
<i>Lama guanicoe</i>	mammal	running	endotherm	89.95	16	55.98	16	herbivore
<i>Lama guanicoe</i>	mammal	running	endotherm	95	7	54.62	7	herbivore
<i>Leggadina forresti</i>	mammal	running	endotherm	0.0155	44	12.25	44	omnivore
<i>Lepus alleni</i>	mammal	running	endotherm	4.4	44	70.04	44	herbivore
<i>Lepus americanus</i>	mammal	running	endotherm	1.5	44	48.55	44	herbivore
<i>Lepus arcticus</i>	mammal	running	endotherm	4.6	44	62.24	44	herbivore
<i>Lepus californicus</i>	mammal	running	endotherm	2	44	62.14	44	herbivore
<i>Lepus europaeus</i>	mammal	running	endotherm	4	44	70.02	44	herbivore
<i>Lepus townsendii</i>	mammal	running	endotherm	3.5	44	54.45	44	herbivore
<i>Liomys pictus</i>	mammal	running	endotherm	0.042	44	16.72	44	omnivore
<i>Lontra canadensis</i>	mammal	running	endotherm	8.09	56	18	85	carnivore
<i>Loxodonta africana</i>	mammal	running	endotherm	8000	101	40.07	101	herbivore
<i>Loxodonta africana</i>	mammal	running	endotherm	6000	34	35	34	herbivore
<i>Loxodonta africana</i>	mammal	running	endotherm	6000	7	34.02	7	herbivore
<i>Lycaon pictus</i>	mammal	running	endotherm	21.98	16	66.07	16	carnivore
<i>Lycaon pictus</i>	mammal	running	endotherm	30	101	72.42	101	carnivore
<i>Lycaon pictus</i>	mammal	running	endotherm	20	44	68.05	44	carnivore
<i>Macropus eugenii</i>	mammal	running	endotherm	4	44	38.88	44	herbivore
<i>Macropus rufus</i>	mammal	running	endotherm	80	101	70	101	herbivore
<i>Macropus spp</i>	mammal	running	endotherm	50	7	38.89	7	herbivore
<i>Macropus spp</i>	mammal	running	endotherm	50	7	58.32	7	herbivore
<i>Macropus spp</i>	mammal	running	endotherm	50	7	97.2	7	herbivore
<i>Macropus spp.</i>	mammal	running	endotherm	50	44	63.33	44	herbivore
<i>Madoqua kirki</i>	mammal	running	endotherm	5.11	16	41.98	16	herbivore
<i>Madoqua kirki</i>	mammal	running	endotherm	5	7	40.82	7	herbivore
<i>Marmota monax</i>	mammal	running	endotherm	4	44	15.55	44	herbivore
<i>Meles meles</i>	mammal	running	endotherm	11.6	44	29.17	44	carnivore
<i>Mephitis mephitis</i>	mammal	running	endotherm	2.5	44	15.55	44	omnivore
<i>Mesocricetus brandti</i>	mammal	running	endotherm	0.11	44	8.75	44	herbivore
<i>Microdipodops megacephalus</i>	mammal	running	endotherm	0.0123	44	10.60	44	omnivore
<i>Microtus pennsylvanicus</i>	mammal	running	endotherm	0.05	44	10.68	44	herbivore
<i>Microtus pinetorum</i>	mammal	running	endotherm	0.03	44	6.60	44	herbivore

<i>Monodelphis brevicaudata</i>	mammal	running	endotherm	0.0745	44	11.37	44	carnivore
<i>Mus musculus</i>	mammal	running	endotherm	0.019	101	13	101	omnivore
<i>Mus musculus</i>	mammal	running	endotherm	0.016	44	12.64	44	omnivore
<i>Myrmecobius fasciatus</i>	mammal	running	endotherm	0.48	44	13.54	44	carnivore
<i>Napaeozapus insignis</i>	mammal	running	endotherm	0.025	44	8.36	44	omnivore
<i>Nasua narica</i>	mammal	running	endotherm	4.4	44	26.24	44	omnivore
<i>Nasua nasua</i>	mammal	running	endotherm	3.40	16	26.98	16	omnivore
<i>Neotoma lepida</i>	mammal	running	endotherm	0.1106	44	16.62	44	herbivore
<i>Notomys alexis</i>	mammal	running	endotherm	0.0245	44	12.73	44	omnivore
<i>Notomys cervinus</i>	mammal	running	endotherm	0.035	44	13.66	44	omnivore
<i>Odocoileus hemionus</i>	mammal	running	endotherm	54.95	16	63.97	16	herbivore
<i>Odocoileus hemionus</i>	mammal	running	endotherm	120	34	61	34	herbivore
<i>Odocoileus virginianus</i>	mammal	running	endotherm	61.94	16	63.97	16	herbivore
<i>Odocoileus virginianus</i>	mammal	running	endotherm	80	101	48.2	101	herbivore
<i>Onychomys torridus</i>	mammal	running	endotherm	0.0193	44	10.06	44	omnivore
<i>Oreamnos americanus</i>	mammal	running	endotherm	119.95	16	33.04	16	herbivore
<i>Oreamnos americanus</i>	mammal	running	endotherm	113.5	7	32.05	7	herbivore
<i>Oryctolagus cuniculus</i>	mammal	running	endotherm	1.9	44	54.432	44	herbivore
<i>Ourebia ourebi</i>	mammal	running	endotherm	14.49	16	50.00	16	herbivore
<i>Ovibos moschatus</i>	mammal	running	endotherm	209.89	16	39.99	16	herbivore
<i>Ovis ammon</i>	mammal	running	endotherm	114.02	16	59.98	16	herbivore
<i>Ovis ammon</i>	mammal	running	endotherm	65	7	58.32	7	herbivore
<i>Ovis canadensis</i>	mammal	running	endotherm	95.06	16	47.97	16	herbivore
<i>Panthera leo</i>	mammal	running	endotherm	169.82	16	54.95	16	carnivore
<i>Panthera leo</i>	mammal	running	endotherm	200	101	80	101	carnivore
<i>Panthera leo</i>	mammal	running	endotherm	155.80	7	57.35	7	carnivore
<i>Panthera pardus</i>	mammal	running	endotherm	51.05	16	59.98	16	carnivore
<i>Panthera pardus</i>	mammal	running	endotherm	52.4	44	58.32	44	carnivore
<i>Panthera tigris</i>	mammal	running	endotherm	144.88	16	55.98	16	carnivore
<i>Panthera tigris</i>	mammal	running	endotherm	161	7	54.43	7	carnivore
<i>Pecari tajacu</i>	mammal	running	endotherm	21.98	16	34.99	16	omnivore
<i>Perognathus longimembris</i>	mammal	running	endotherm	0.0089	44	9.62	44	omnivore
<i>Perognathus parvus</i>	mammal	running	endotherm	0.0244	44	12.15	44	herbivore

<i>Peromyscus crinitus</i>	mammal	running	endotherm	0.0137	44	11.08	44	omnivore
<i>Peromyscus eremicus</i>	mammal	running	endotherm	0.0198	44	12.73	44	omnivore
<i>Peromyscus leucopus</i>	mammal	running	endotherm	0.025	44	10.69	44	omnivore
<i>Peromyscus maniculatus</i>	mammal	running	endotherm	0.0182	44	13.03	44	omnivore
<i>Peromyscus maniculatus</i>	mammal	running	endotherm	0.022	11	9	11	omnivore
<i>Peromyscus truei</i>	mammal	running	endotherm	0.0193	44	13.90	44	herbivore
<i>Phacochoerus aethiopicus</i>	mammal	running	endotherm	87.90	16	54.95	16	herbivore
<i>Phacochoerus aethiopicus</i>	mammal	running	endotherm	85	7	46.77	7	herbivore
<i>Phacochoerus aethiopicus</i>	mammal	running	endotherm	85	7	53.48	7	herbivore
<i>Potorous tridactylus</i>	mammal	running	endotherm	0.998	44	20.80	44	omnivore
<i>Potorous tridactylus</i>	mammal	running	endotherm	0.998	7	20.80	7	omnivore
<i>Presbytis</i>	mammal	running	endotherm	13	44	35.97	44	herbivore
<i>Procyon lotor</i>	mammal	running	endotherm	7.50	16	10.91	16	omnivore
<i>Procyon lotor</i>	mammal	running	endotherm	7	44	23.35	44	omnivore
<i>Pseudomys australis</i>	mammal	running	endotherm	0.05	44	15.92	44	omnivore
<i>Pseudomys hermannsburgensis</i>	mammal	running	endotherm	0.018	44	12.25	44	omnivore
<i>Pseudomys nanus</i>	mammal	running	endotherm	0.061	44	14.05	44	herbivore
<i>Rangifer tarandus</i>	mammal	running	endotherm	159.96	16	69.98	16	herbivore
<i>Rangifer tarandus</i>	mammal	running	endotherm	120	34	80	34	herbivore
<i>Rangifer tarandus</i>	mammal	running	endotherm	100	7	77.79	7	herbivore
<i>Rattus</i>	mammal	running	endotherm	0.25	44	9.43	44	omnivore
<i>Rupicapra pyrenaica</i>	mammal	running	endotherm	33.96	16	50.00	16	herbivore
<i>Rupicapra rupicapra</i>	mammal	running	endotherm	38.02	16	50.00	16	herbivore
<i>Rupicapra rupicapra</i>	mammal	running	endotherm	50	34	50	34	herbivore
<i>Saiga tatarica</i>	mammal	running	endotherm	26.18	16	74.99	16	herbivore
<i>Saiga tatarica</i>	mammal	running	endotherm	35	34	80	34	herbivore
<i>Saiga tatarica</i>	mammal	running	endotherm	35	7	77.76	7	herbivore
<i>Sciurus carolinensis</i>	mammal	running	endotherm	0.5	44	29.11	44	herbivore
<i>Sciurus carolinensis</i>	mammal	running	endotherm	0.133	101	20	101	omnivore
<i>Sciurus carolinensis</i>	mammal	running	endotherm	0.479	11	27.36	11	omnivore
<i>Sciurus niger</i>	mammal	running	endotherm	1.078	44	23.33	44	omnivore
<i>Sciurus vulgaris</i>	mammal	running	endotherm	0.4	44	19.46	44	herbivore
<i>Sminthopsis crassicaudata</i>	mammal	running	endotherm	0.017	44	11.18	44	carnivore

<i>Sminthopsis macroura</i>	mammal	running	endotherm	0.02	44	14.03	44	carnivore
<i>Spermophilopsis leptodactylus</i>	mammal	running	endotherm	0.6	44	35.01	44	omnivore
<i>Spermophilus citellus</i>	mammal	running	endotherm	0.5	44	17.47	44	herbivore
<i>Spermophilus saturatus</i>	mammal	running	endotherm	0.222	44	21.53	44	herbivore
<i>Spermophilus tereticaudus</i>	mammal	running	endotherm	0.1126	44	14.78	44	omnivore
<i>Spermophilus tridecemlineatus</i>	mammal	running	endotherm	0.125	44	11.82	44	omnivore
<i>Spermophilus undulatus</i>	mammal	running	endotherm	0.6	44	19.45	44	omnivore
<i>Sus scrofa</i>	mammal	running	endotherm	135	56	56	98	omnivore
<i>Sylvilagus</i>	mammal	running	endotherm	1.5	44	38.88	44	herbivore
<i>Sylvilagus</i>	mammal	running	endotherm	1.5	7	48.55	7	herbivore
<i>Sylvilagus floridanus</i>	mammal	running	endotherm	2	101	48	101	herbivore
<i>Syncerus caffer</i>	mammal	running	endotherm	439.54	16	57.02	16	herbivore
<i>Syncerus caffer</i>	mammal	running	endotherm	620	7	55.44	7	herbivore
<i>Tamias amoenus</i>	mammal	running	endotherm	0.051	44	18.86	44	omnivore
<i>Tamias minimus</i>	mammal	running	endotherm	0.0293	44	16.27	44	herbivore
<i>Tamias striatus</i>	mammal	running	endotherm	0.1	44	16.52	44	herbivore
<i>Tamias striatus</i>	mammal	running	endotherm	0.125	11	17.28	11	herbivore
<i>Tamiasciurus hudsonicus</i>	mammal	running	endotherm	0.22	44	14.62	44	herbivore
<i>Tamiasciurus hudsonicus</i>	mammal	running	endotherm	0.22	7	14.62	7	herbivore
<i>Tapirus terrestris</i>	mammal	running	endotherm	172.98	16	39.99	16	herbivore
<i>Taurotragus derbianus</i>	mammal	running	endotherm	680.77	16	69.98	16	herbivore
<i>Taurotragus oryx</i>	mammal	running	endotherm	559.76	16	69.98	16	herbivore
<i>Taurotragus oryx</i>	mammal	running	endotherm	511	7	68.17	7	herbivore
<i>Tayassu pecari</i>	mammal	running	endotherm	33.04	16	34.99	16	omnivore
<i>Urocyon cinereoargenteus</i>	mammal	running	endotherm	0.3	44	12.61	44	herbivore
<i>Urocyon cinereoargenteus</i>	mammal	running	endotherm	5.8	101	67.6	101	omnivore
<i>Urocyon cinereoargenteus</i>	mammal	running	endotherm	3.7	44	62.21	44	omnivore
<i>Urocyon cinereoargenteus</i>	mammal	running	endotherm	3.80	16	41.98	16	omnivore
<i>Uromys caudimaculatus</i>	mammal	running	endotherm	1.18	44	16.16	44	omnivore
<i>Ursus americanus</i>	mammal	running	endotherm	104.95	16	47.97	16	carnivore
<i>Ursus americanus</i>	mammal	running	endotherm	93.4	44	46.63	44	carnivore
<i>Ursus arctos</i>	mammal	running	endotherm	250	101	35	101	carnivore
<i>Ursus arctos</i>	mammal	running	endotherm	251.3	7	46.66	7	carnivore

<i>Ursus arctos horribilis</i>	mammal	running	endotherm	154.88	16	47.97	16	carnivore
<i>Ursus maritimus</i>	mammal	running	endotherm	174.98	16	50	16	carnivore
<i>Ursus maritimus</i>	mammal	running	endotherm	650	101	30	101	carnivore
<i>Ursus maritimus</i>	mammal	running	endotherm	265	7	38.92	7	carnivore
<i>Vicugna vicugna</i>	mammal	running	endotherm	44.98	16	46.99	16	herbivore
<i>Vulpes vulpes</i>	mammal	running	endotherm	5.50	16	47.97	16	carnivore
<i>Vulpes vulpes</i>	mammal	running	endotherm	4.8	44	70.03	44	carnivore
<i>Vulpes vulpes</i>	mammal	running	endotherm	4.59	11	72	11	carnivore
<i>Zapus hudsonicus</i>	mammal	running	endotherm	0.018	44	8.65	44	omnivore
<i>Zapus trinitatus</i>	mammal	running	endotherm	0.0285	44	13.84	44	omnivore
<i>Zyzomys argurus</i>	mammal	running	endotherm	0.0605	44	12.05	44	omnivore
<i>Acanthodactylus erythrurus</i>	reptile	running	ectotherm	0.0089	80	11.27	80	carnivore
<i>Acanthodactylus pardalis</i>	reptile	running	ectotherm	0.0067	80	9.42	80	carnivore
<i>Acanthodactylus scutellatus</i>	reptile	running	ectotherm	0.00784	27	11.95	27	carnivore
<i>Acanthodactylus scutellatus</i>	reptile	running	ectotherm	0.0081	80	10.06	80	carnivore
<i>Amblyrhynchus cristatus</i>	reptile	running	ectotherm	0.0718	80	10.08	80	herbivore
<i>Anolis carolinensis</i>	reptile	running	ectotherm	0.006	80	4.32	80	carnivore
<i>Anolis cristatellus</i>	reptile	running	ectotherm	0.0081	80	7.76	80	carnivore
<i>Anolis evermanni</i>	reptile	running	ectotherm	0.0056	80	6.57	80	carnivore
<i>Anolis frenatus</i>	reptile	running	ectotherm	0.0427	80	9.78	80	carnivore
<i>Anolis gundlachi</i>	reptile	running	ectotherm	0.0071	80	7.76	80	carnivore
<i>Anolis humilis</i>	reptile	running	ectotherm	0.001	80	4.18	80	carnivore
<i>Anolis krugi</i>	reptile	running	ectotherm	0.0024	80	6.43	80	carnivore
<i>Anolis lemurinus</i>	reptile	running	ectotherm	0.0036	80	5.33	80	carnivore
<i>Anolis limifrons</i>	reptile	running	ectotherm	9.00E-04	80	4.75	80	carnivore
<i>Anolis lineatopus</i>	reptile	running	ectotherm	0.0046	80	7.32	80	carnivore
<i>Anolis poncensis</i>	reptile	running	ectotherm	0.0016	80	6.34	80	carnivore
<i>Anolis pulchellus</i>	reptile	running	ectotherm	0.0015	80	6.12	80	carnivore
<i>Anolis sagrei</i>	reptile	running	ectotherm	0.0029	80	6.52	80	carnivore
<i>Anolis stratulus</i>	reptile	running	ectotherm	0.0019	80	5.36	80	carnivore
<i>Aspidoscelis tigris</i>	reptile	running	ectotherm	0.01142	27	15.37	27	carnivore
<i>Callisaurus draconoides</i>	reptile	running	ectotherm	0.0982	11	25.92	11	carnivore
<i>Callisaurus draconoides</i>	reptile	running	ectotherm	0.01193	27	17.32	27	carnivore

<i>Carlia fusca</i>	reptile	running	ectotherm	0.00335	27	6.23	27	carnivore
<i>Christinus marmoratus</i>	reptile	running	ectotherm	0.0037	80	3.49	80	carnivore
<i>Cnemidophorus inornatus arizonae</i>	reptile	running	ectotherm	0.0042	80	8.15	80	carnivore
<i>Cnemidophorus inornatus heptagrammus</i>	reptile	running	ectotherm	0.004	80	6.75	80	carnivore
<i>Cnemidophorus sexlineatus</i>	reptile	running	ectotherm	0.2	101	29	101	carnivore
<i>Cnemidophorus tigris marmoratus</i>	reptile	running	ectotherm	0.0179	80	8.64	80	carnivore
<i>Cnemidophorus tigris punctilinealis</i>	reptile	running	ectotherm	0.0112	80	9.53	80	carnivore
<i>Coleonyx brevis</i>	reptile	running	ectotherm	0.0018	80	5.36	80	carnivore
<i>Coleonyx variegatus</i>	reptile	running	ectotherm	0.0044	80	5.51	80	carnivore
<i>Cophosaurus texanus</i>	reptile	running	ectotherm	0.00994	27	13.72	27	carnivore
<i>Crotaphytus collaris</i>	reptile	running	ectotherm	0.04015	27	12.10	27	carnivore
<i>Ctenophorus nuchalis</i>	reptile	running	ectotherm	0.0138	80	9.23	80	omnivore
<i>Ctenotus regius</i>	reptile	running	ectotherm	0.0055	80	3.56	80	carnivore
<i>Ctenotus taeniolatus</i>	reptile	running	ectotherm	0.0045	80	4.25	80	carnivore
<i>Ctenotus uber</i>	reptile	running	ectotherm	0.0054	80	5.94	80	carnivore
<i>Dendroaspis polylepis</i>	reptile	running	ectotherm	1.4	101	23	73	carnivore
<i>Dendroaspis polylepis</i>	reptile	running	ectotherm	1.4	101	32.2	101	carnivore
<i>Dipsosaurus dorsalis</i>	reptile	running	ectotherm	0.398	11	26.28	11	herbivore
<i>Egernia cunninghami</i>	reptile	running	ectotherm	0.268	80	9.69	80	herbivore
<i>Egernia whitii</i>	reptile	running	ectotherm	0.0251	80	3.92	80	omnivore
<i>Elgaria kingii</i>	reptile	running	ectotherm	0.00973	27	4.21	27	carnivore
<i>Eremias lineoocellata</i>	reptile	running	ectotherm	0.0042	80	9.47	80	carnivore
<i>Eremias lugubris</i>	reptile	running	ectotherm	0.004	80	5.69	80	carnivore
<i>Eremias namaquensis</i>	reptile	running	ectotherm	0.0025	80	9.65	80	carnivore
<i>Eremiascincus fasciolatus</i>	reptile	running	ectotherm	0.0125	80	2.99	80	carnivore
<i>Eublepharis macularius</i>	reptile	running	ectotherm	0.0495	80	2.38	80	carnivore
<i>Eulamprus kosciuskoi</i>	reptile	running	ectotherm	0.0083	80	3.74	80	carnivore
<i>Eulamprus quoyi</i>	reptile	running	ectotherm	0.0211	80	5.47	80	carnivore
<i>Eulamprus tympanum</i>	reptile	running	ectotherm	0.0144	80	5.36	80	carnivore
<i>Gallotia atlantica</i>	reptile	running	ectotherm	0.0054	80	6.55	80	omnivore
<i>Gallotia caesaris</i>	reptile	running	ectotherm	0.0098	80	7.74	80	omnivore
<i>Gallotia simonyi</i>	reptile	running	ectotherm	0.23	80	8.28	80	omnivore
<i>Gallotia stehlini</i>	reptile	running	ectotherm	0.208	80	11.34	80	omnivore

<i>Gambelia wislizenii</i>	reptile	running	ectotherm	0.01981	27	11.81	27	omnivore
<i>Gekko gecko</i>	reptile	running	ectotherm	0.0381	80	5.44	80	carnivore
<i>Gonatodes concinnatus</i>	reptile	running	ectotherm	0.0023	80	3.74	80	carnivore
<i>Hemidactylus frenatus</i>	reptile	running	ectotherm	0.0033	80	7.96	80	carnivore
<i>Hemidactylus turcicus</i>	reptile	running	ectotherm	0.0028	80	5.90	80	carnivore
<i>Hemiergis decresiensis</i>	reptile	running	ectotherm	8.00E-04	80	2.30	80	carnivore
<i>Hemiergis peronii</i>	reptile	running	ectotherm	0.0015	80	1.76	80	carnivore
<i>Holbrookia elegans</i>	reptile	running	ectotherm	0.00405	27	10.62	27	carnivore
<i>Lacerta agilis</i>	reptile	running	ectotherm	0.0091	80	6.04	80	carnivore
<i>Lacerta bedriagae</i>	reptile	running	ectotherm	0.0096	80	6.43	80	carnivore
<i>Lacerta monticola</i>	reptile	running	ectotherm	0.0077	80	5.64	80	carnivore
<i>Lacerta schreiberi</i>	reptile	running	ectotherm	0.0212	80	6.43	80	carnivore
<i>Lacerta viridis</i>	reptile	running	ectotherm	0.0284	80	9.64	80	carnivore
<i>Lacerta vivipara</i>	reptile	running	ectotherm	0.0028	80	3.24	80	carnivore
<i>Laudakia stellio</i>	reptile	running	ectotherm	0.04854	27	10.91	27	carnivore
<i>Laudakia stellio</i>	reptile	running	ectotherm	0.0401	80	9.72	80	carnivore
<i>Laudakia stellio</i>	reptile	running	ectotherm	0.0411	80	9	80	carnivore
<i>Laudakia stellio</i>	reptile	running	ectotherm	0.0419	80	8.28	80	carnivore
<i>Laudakia stellio</i>	reptile	running	ectotherm	0.0551	80	8.64	80	carnivore
<i>Leiolepis belliana</i>	reptile	running	ectotherm	0.04	80	7.92	80	omnivore
<i>Lepidodactylus lugubris</i>	reptile	running	ectotherm	0.0011	80	5.54	80	carnivore
<i>Nucras tessellata</i>	reptile	running	ectotherm	0.0047	80	7.38	80	carnivore
<i>Petrosaurus mearnsi</i>	reptile	running	ectotherm	0.0113	80	8.46	80	omnivore
<i>Phrynosoma cornutum</i>	reptile	running	ectotherm	0.03362	27	6.34	27	carnivore
<i>Phrynosoma mcallii</i>	reptile	running	ectotherm	0.01146	27	5.54	27	carnivore
<i>Phrynosoma modestum</i>	reptile	running	ectotherm	0.00595	27	4.5	27	carnivore
<i>Phrynosoma platyrhinos</i>	reptile	running	ectotherm	0.01626	27	5.58	27	carnivore
<i>Plestiodon fasciatus</i>	reptile	running	ectotherm	0.00735	27	6.48	27	carnivore
<i>Plestiodon skiltonianus</i>	reptile	running	ectotherm	0.0052	80	2.74	80	carnivore
<i>Podarcis bocagei</i>	reptile	running	ectotherm	0.0033	80	5.12	80	carnivore
<i>Podarcis hispanica</i>	reptile	running	ectotherm	0.0025	80	7.30	80	carnivore
<i>Podarcis hispanica atrata</i>	reptile	running	ectotherm	0.0076	80	5.50	80	carnivore
<i>Podarcis lilfordi</i>	reptile	running	ectotherm	0.0078	80	8.41	80	carnivore

<i>Podarcis muralis</i>	reptile	running	ectotherm	0.0031	80	7.69	80	carnivore
<i>Podarcis pityusensis</i>	reptile	running	ectotherm	0.0098	80	9.14	80	carnivore
<i>Podarcis sicula</i>	reptile	running	ectotherm	0.00539	27	8.64	27	carnivore
<i>Podarcis sicula</i>	reptile	running	ectotherm	0.0071	80	6.01	80	carnivore
<i>Podarcis tiliguerta</i>	reptile	running	ectotherm	0.0048	80	8.68	80	carnivore
<i>Psammodromus algirus</i>	reptile	running	ectotherm	0.011	80	9.09	80	carnivore
<i>Psammodromus hispanicus</i>	reptile	running	ectotherm	0.0014	80	5.40	80	carnivore
<i>Pseudemoia entrecasteauxii</i>	reptile	running	ectotherm	0.0033	80	3.20	80	carnivore
<i>Pseudemoia entrecasteauxii</i>	reptile	running	ectotherm	0.0047	80	4.25	80	carnivore
<i>Sceloporus clarkii</i>	reptile	running	ectotherm	0.012	80	6.80	80	carnivore
<i>Sceloporus cowlesi</i>	reptile	running	ectotherm	0.00451	27	7.92	27	carnivore
<i>Sceloporus graciosus</i>	reptile	running	ectotherm	0.00703	27	8.35	27	carnivore
<i>Sceloporus jarrovi</i>	reptile	running	ectotherm	0.0153	80	6.23	80	carnivore
<i>Sceloporus magister</i>	reptile	running	ectotherm	0.03101	27	11.20	27	carnivore
<i>Sceloporus merriami</i>	reptile	running	ectotherm	0.0042	80	7.01	80	carnivore
<i>Sceloporus merriami</i>	reptile	running	ectotherm	0.0048	80	7.64	80	carnivore
<i>Sceloporus occidentalis</i>	reptile	running	ectotherm	0.0074	80	6.95	80	carnivore
<i>Sceloporus undulatus</i>	reptile	running	ectotherm	0.0056	80	6.23	80	carnivore
<i>Sceloporus undulatus</i>	reptile	running	ectotherm	0.0059	80	5.83	80	carnivore
<i>Sceloporus undulatus hyacinthus</i>	reptile	running	ectotherm	0.01	80	7.70	80	carnivore
<i>Sceloporus virgatus</i>	reptile	running	ectotherm	0.00523	27	6.34	27	carnivore
<i>Sceloporus woodi</i>	reptile	running	ectotherm	0.0028	80	8.93	80	carnivore
<i>Scincella lateralis</i>	reptile	running	ectotherm	8.00E-04	80	1.37	80	carnivore
<i>Takydromus septentrionalis</i>	reptile	running	ectotherm	0.0055	80	2.92	80	carnivore
<i>Tiliqua scincoides</i>	reptile	running	ectotherm	0.438	80	3.85	80	omnivore
<i>Trachylepis occidentalis</i>	reptile	running	ectotherm	0.0137	80	6.23	80	carnivore
<i>Trachylepis spilogaster</i>	reptile	running	ectotherm	0.0095	80	8.53	80	carnivore
<i>Trachylepis striata</i>	reptile	running	ectotherm	0.0158	80	7.56	80	carnivore
<i>Trachylepis variegata</i>	reptile	running	ectotherm	0.0013	80	4.90	80	carnivore
<i>Trapelus savignyi</i>	reptile	running	ectotherm	0.022	80	9.72	80	carnivore
<i>Uma rufopunctata</i>	reptile	running	ectotherm	0.02967	27	11.92	27	carnivore
<i>Uma scoparia</i>	reptile	running	ectotherm	0.0185	80	8.57	80	carnivore
<i>Urosaurus graciosus</i>	reptile	running	ectotherm	0.0036	80	6.37	80	carnivore

<i>Urosaurus nigricaudus</i>	reptile	running	ectotherm	0.0023	80	6.44	80	carnivore
<i>Urosaurus ornatus</i>	reptile	running	ectotherm	0.00347	27	8.24	27	carnivore
<i>Urosaurus ornatus</i>	reptile	running	ectotherm	0.0035	80	7.60	80	carnivore
<i>Uta stansburiana</i>	reptile	running	ectotherm	0.00383	27	7.81	27	carnivore
<i>Uta stansburiana</i>	reptile	running	ectotherm	0.003	80	6.66	80	carnivore
<i>Varanus acanthurus</i>	reptile	running	ectotherm	0.0589	18	10.98	18	carnivore
<i>Varanus brevicauda</i>	reptile	running	ectotherm	0.0206	18	5.72	18	carnivore
<i>Varanus caudolineatus</i>	reptile	running	ectotherm	0.0181	18	8.42	18	carnivore
<i>Varanus eremius</i>	reptile	running	ectotherm	0.0485	18	13.36	18	carnivore
<i>Varanus giganteus</i>	reptile	running	ectotherm	2.9667	18	31.57	18	carnivore
<i>Varanus gilleni</i>	reptile	running	ectotherm	0.0271	18	8.028	18	carnivore
<i>Varanus glauerti</i>	reptile	running	ectotherm	0.0357	18	11.12	18	carnivore
<i>Varanus gouldii</i>	reptile	running	ectotherm	0.4294	18	20.59	18	carnivore
<i>Varanus kingorum</i>	reptile	running	ectotherm	0.0183	18	9.36	18	carnivore
<i>Varanus mertensi</i>	reptile	running	ectotherm	1.0323	18	12.85	18	carnivore
<i>Varanus mitchelli</i>	reptile	running	ectotherm	0.1513	18	12.35	18	carnivore
<i>Varanus panoptes</i>	reptile	running	ectotherm	2.425	18	21.24	18	carnivore
<i>Varanus pilbarensis</i>	reptile	running	ectotherm	0.0303	18	10.19	18	carnivore
<i>Varanus rosenbergi</i>	reptile	running	ectotherm	1.025	18	18.97	18	carnivore
<i>Varanus scalaris</i>	reptile	running	ectotherm	0.1021	18	9.94	18	carnivore
<i>Varanus storri</i>	reptile	running	ectotherm	0.0269	18	9.18	18	carnivore
<i>Varanus tristis</i>	reptile	running	ectotherm	0.0983	18	14.22	18	carnivore
<i>Varanus varius</i>	reptile	running	ectotherm	7.7	18	14.51	18	carnivore
<i>Euphausia superba</i>	arthropod	swimming	ectotherm	0.002	91	1.66	48	herbivore
<i>Aptenodytes forsteri</i>	bird	swimming	endotherm	29.75	56	10.8	49	carnivore
<i>Aptenodytes patagonicus</i>	bird	swimming	endotherm	14	101	12.1	101	carnivore
<i>Pygoscelis adeliae</i>	bird	swimming	endotherm	3.36	11	13.68	11	carnivore
<i>Pygoscelis antarcticus</i>	bird	swimming	endotherm	4.5	101	32	101	carnivore
<i>Pygoscelis papua</i>	bird	swimming	endotherm	8.2	101	36	101	carnivore
<i>Acanthocybium solandri</i>	fish	swimming	ectotherm	13.31	11	77.4	11	carnivore
<i>Acanthocybium solandri</i>	fish	swimming	ectotherm	16.64	79	77	101	carnivore
<i>Alburnus alburnus</i>	fish	swimming	ectotherm	0.001	5	1.8	5	carnivore
<i>Alosa finita</i>	fish	swimming	ectotherm	0.0297	5	2.7	5	carnivore

<i>Alosa pseudoharengus</i>	fish	swimming	ectotherm	0.27	11	15.84	11	carnivore
<i>Anguilla anguilla</i>	fish	swimming	ectotherm	2.16	8	4.1	8	carnivore
<i>Argyrosomus regius</i>	fish	swimming	ectotherm	0.0295	5	4.07	5	carnivore
<i>Barbatula barbatula</i>	fish	swimming	ectotherm	0.0177	78	3.89	78	carnivore
<i>Carassius auratus</i>	fish	swimming	ectotherm	0.00343	11	2.7	11	carnivore
<i>Carassius auratus</i>	fish	swimming	ectotherm	0.020	8	10.8	8	carnivore
<i>Carassius auratus</i>	fish	swimming	ectotherm	0.276	6	7.2	6	carnivore
<i>Carassius leucas</i>	fish	swimming	ectotherm	9.53	5	14.59	5	carnivore
<i>Carassius leucas</i>	fish	swimming	ectotherm	40.07	5	18.76	5	carnivore
<i>Carcharodon carcharias</i>	fish	swimming	ectotherm	800	101	40	101	carnivore
<i>Clupea harengus</i>	fish	swimming	ectotherm	0.15625	8	6.12	8	carnivore
<i>Clupea harengus</i>	fish	swimming	ectotherm	7.57E-05	90	0.5004	90	carnivore
<i>Clupea harengus</i>	fish	swimming	ectotherm	1.30E-04	90	0.5472	90	carnivore
<i>Cottus gobio</i>	fish	swimming	ectotherm	0.0190	78	4.032	78	carnivore
<i>Cottus gobio</i>	fish	swimming	ectotherm	0.0688	78	4.92	78	carnivore
<i>Cyprinus carpio</i>	fish	swimming	ectotherm	0.0483	78	3.72	78	omnivore
<i>Cyprinus carpio</i>	fish	swimming	ectotherm	0.3277	78	4.83	78	omnivore
<i>Cyprinus carpio</i>	fish	swimming	ectotherm	0.0055	5	2.00	5	omnivore
<i>Cyprinus carpio</i>	fish	swimming	ectotherm	0.087	5	6.12	5	omnivore
<i>Esox lucius</i>	fish	swimming	ectotherm	0.145	5	7.56	5	carnivore
<i>Esox lucius</i>	fish	swimming	ectotherm	1.18	5	5.33	5	carnivore
<i>Gadus morhua</i>	fish	swimming	ectotherm	1.76	8	7.56	8	carnivore
<i>Gadus morhua</i>	fish	swimming	ectotherm	2.18E-05	90	0.288	90	carnivore
<i>Galeocerdo cuvier</i>	fish	swimming	ectotherm	550	101	32	101	carnivore
<i>Helicolenus dactylopterus</i>	fish	swimming	ectotherm	0.493	5	3.53	5	carnivore
<i>Istiompax indica</i>	fish	swimming	ectotherm	150	10	130	10	carnivore
<i>Istiophorus albicans</i>	fish	swimming	ectotherm	90	101	110	101	carnivore
<i>Istiophorus albicans</i>	fish	swimming	ectotherm	90	101	108	10	carnivore
<i>Isurus oxyrinchus</i>	fish	swimming	ectotherm	105	101	67.68	103	carnivore
<i>Isurus oxyrinchus</i>	fish	swimming	ectotherm	300	101	50	101	carnivore
<i>Leuciscus leuciscus</i>	fish	swimming	ectotherm	0.01	11	4.68	11	herbivore
<i>Leuciscus leuciscus</i>	fish	swimming	ectotherm	0.03375	11	6.3	11	herbivore
<i>Leuciscus leuciscus</i>	fish	swimming	ectotherm	0.08	11	7.92	11	herbivore

<i>Leuciscus leuciscus</i>	fish	swimming	ectotherm	0.279	6	8.64	6	herbivore
<i>Leuciscus leuciscus</i>	fish	swimming	ectotherm	0.184	5	6.12	5	herbivore
<i>Makaira nigricans</i>	fish	swimming	ectotherm	153.5	95	75	10	carnivore
<i>Melanogrammus aeglefinus</i>	fish	swimming	ectotherm	0.741	8	6.48	8	carnivore
<i>Merlangius merlangus</i>	fish	swimming	ectotherm	0.08	8	5.76	8	carnivore
<i>Merluccius merluccius</i>	fish	swimming	ectotherm	0.0237	5	2.84	5	carnivore
<i>Micropterus salmoides</i>	fish	swimming	ectotherm	0.276	5	3.17	5	carnivore
<i>Mugil cephalus</i>	fish	swimming	ectotherm	0.026	5	2.20	5	omnivore
<i>Perca fluviatilis</i>	fish	swimming	ectotherm	0.0184	5	2.38	5	carnivore
<i>Platichthys flesus</i>	fish	swimming	ectotherm	1.21E-05	90	0.234	90	carnivore
<i>Pleuronectes platessa</i>	fish	swimming	ectotherm	3.57E-04	11	0.2304	11	carnivore
<i>Pleuronectes platessa</i>	fish	swimming	ectotherm	5.71E-04	11	0.4104	11	carnivore
<i>Pleuronectes platessa</i>	fish	swimming	ectotherm	0.15625	8	4.64	8	carnivore
<i>Pollachius virens</i>	fish	swimming	ectotherm	0.266	8	7.2	8	carnivore
<i>Rutilus rutilus</i>	fish	swimming	ectotherm	0.0057	78	2.34	78	omnivore
<i>Rutilus rutilus</i>	fish	swimming	ectotherm	0.1275	78	5.02	78	omnivore
<i>Salmo irideus</i>	fish	swimming	ectotherm	0.551	6	9.72	6	carnivore
<i>Salmo irideus</i>	fish	swimming	ectotherm	0.235	5	6.12	5	carnivore
<i>Salmo salar</i>	fish	swimming	ectotherm	0.0023	5	0.472	5	carnivore
<i>Salmo salar</i>	fish	swimming	ectotherm	0.0048	5	0.601	5	carnivore
<i>Salmo salar</i>	fish	swimming	ectotherm	0.0078	5	0.778	5	carnivore
<i>Salmo salar</i>	fish	swimming	ectotherm	6.66	5	21.6	5	carnivore
<i>Salmo salar</i>	fish	swimming	ectotherm	7.85	5	17.532	5	carnivore
<i>Salmo trutta</i>	fish	swimming	ectotherm	0.12167	8	8.424	8	carnivore
<i>Salmo trutta</i>	fish	swimming	ectotherm	0.54872	8	11.52	8	carnivore
<i>Salmo trutta</i>	fish	swimming	ectotherm	0.0341	5	3.312	5	carnivore
<i>Salmo trutta fario</i>	fish	swimming	ectotherm	0.0217	78	4.54	78	carnivore
<i>Salmo trutta fario</i>	fish	swimming	ectotherm	0.969	5	12.6	5	carnivore
<i>Scardinius erythrophthalmus</i>	fish	swimming	ectotherm	0.0188	5	4.104	5	omnivore
<i>Scardinius erythrophthalmus</i>	fish	swimming	ectotherm	0.299	5	4.68	5	omnivore
<i>Scomber scombrus</i>	fish	swimming	ectotherm	0.54872	8	5.72	8	carnivore
<i>Scomber scombrus</i>	fish	swimming	ectotherm	0.0252	5	2.92	5	carnivore
<i>Sphyræna argentea</i>	fish	swimming	ectotherm	4.5	101	44	101	carnivore

<i>Sphyræna barracuda</i>	fish	swimming	ectotherm	26.56	5	43.89	5	carnivore
<i>Squalinus cephalus</i>	fish	swimming	ectotherm	0.0015	5	0.864	5	omnivore
<i>Tetrapturus audax</i>	fish	swimming	ectotherm	163	101	81	101	carnivore
<i>Thunnus albacares</i>	fish	swimming	ectotherm	9.41	11	74.88	11	carnivore
<i>Thunnus albacares</i>	fish	swimming	ectotherm	13.11	82	75	82	carnivore
<i>Thunnus orientalis</i>	fish	swimming	ectotherm	250	101	70	101	carnivore
<i>Thunnus thynnus</i>	fish	swimming	ectotherm	27.22	5	70.81	5	carnivore
<i>Trachinus vipera</i>	fish	swimming	ectotherm	0.0224	5	1.44	5	carnivore
<i>Trigla sp</i>	fish	swimming	ectotherm	0.21	5	4.72	5	carnivore
<i>Trisopterus luscus</i>	fish	swimming	ectotherm	0.0165	5	1.98	5	carnivore
<i>Xiphias gladius</i>	fish	swimming	ectotherm	98	101	97	101	carnivore
<i>Balaenoptera musculus</i>	mammal	swimming	endotherm	108400	11	37.08	11	carnivore
<i>Delphinapterus leucas</i>	mammal	swimming	endotherm	1380	56	22	59	carnivore
<i>Delphinus delphis</i>	mammal	swimming	endotherm	118	68	28.8	68	carnivore
<i>Delphinus delphis</i>	mammal	swimming	endotherm	95.32	11	37.08	11	carnivore
<i>Enhydra lutris</i>	mammal	swimming	endotherm	30	101	9	101	carnivore
<i>Megaptera novaeangliae</i>	mammal	swimming	endotherm	30000	101	27	101	carnivore
<i>Megaptera novaeangliae</i>	mammal	swimming	endotherm	30000	56	23.3	58	carnivore
<i>Orcinus orca</i>	mammal	swimming	endotherm	4100	101	48	101	carnivore
<i>Orcinus orca</i>	mammal	swimming	endotherm	4300	56	25	63	carnivore
<i>Orcinus orca</i>	mammal	swimming	endotherm	4300	56	55.44	99	carnivore
<i>Physeter catodon</i>	mammal	swimming	endotherm	10100	56	39	84	carnivore
<i>Pseudorca crassidens</i>	mammal	swimming	endotherm	1378.5	68	28.8	68	carnivore
<i>Pusa hispida</i>	mammal	swimming	endotherm	88.07	56	30	100	carnivore
<i>Tursiops truncatus</i>	mammal	swimming	endotherm	250	101	35	101	carnivore
<i>Tursiops truncatus</i>	mammal	swimming	endotherm	250	68	29.5	68	carnivore
<i>Zalophus californianus</i>	mammal	swimming	endotherm	158	56	40	97	carnivore
<i>Aequipecten opercularis</i>	mollusc	swimming	ectotherm	0.0143	50	0.9	72	omnivore
<i>Illex illecebrosus</i>	mollusc	swimming	ectotherm	0.6	61	5.04	61	carnivore
<i>Loligo vulgaris</i>	mollusc	swimming	ectotherm	0.35	72	7.2	72	carnivore
<i>Octopus vulgaris</i>	mollusc	swimming	ectotherm	17	101	40	101	carnivore
<i>Sepia officinalis</i>	mollusc	swimming	ectotherm	0.25	72	2.88	72	carnivore
<i>Dermochelys coriacea</i>	reptile	swimming	ectotherm	420	56	35.28	99	carnivore

When only body length was given, the following mass-lengths regressions were used to calculate body mass:

<i>terrestrial arthropods</i>	Jurkschat L. Allometric scaling relationships in the morphology of temperate and tropical arthropods. Master's Thesis. Univ. of Göttingen (2015)
<i>others</i>	Peters, R. H. <i>The ecological implications of body size</i> . 2 , (Cambridge University Press, 1986).

References

peer reviewed

- 1 Amaya, C. C., Klawinski, P. D. & Formanowicz, J., Daniel R. The Effects of Leg Autotomy on Running Speed and Foraging Ability in Two Species of Wolf Spider, (Lycosidae). *Am. Midl. Nat.* 145, 201–205 (2001).
- 2 Apontes, P. & Brown, C. A. Between-sex variation in running speed and a potential cost of leg autotomy in the wolf spider *Pirata sedentarius* . *Am. Midl. Nat.* **154**, 115–125 (2005).
- 3 Auerbach, P. S. *Wilderness Medicine: Expert Consult Premium Edition - Enhanced Online Features* . (Elsevier Health Sciences, 2011).
- 4 Azuma, A. & Watanabe, T. Flight performance of a dragonfly. *J. Exp. Biol.* **137**, 221–252 (1988).
- 5 Bainbridge, R. The speed of swimming of fish as related to size and to the frequency and amplitude of the tail beat. *J. Exp. Biol.* **35**, 109–133 (1958).
- 6 Bainbridge, R. Speed and stamina in three fish. *J. Exp. Biol.* **37**, 129–153 (1960).
- 7 Bejan, A. & Marden, J. H. Unifying constructal theory for scale effects in running, swimming and flying. *J. Exp. Biol.* **209**, 238–248 (2006).
- 8 Blaxter, J. H. S. & Dickson, W. Observations on the swimming speeds of fish. *J. Cons.* **24**, 472–479 (1959).
- 9 Bleckmann, H. & Barth, F. G. Sensory ecology of a semi-aquatic spider (*Dolomedes triton*). *Behav. Ecol. Sociobiol.* 14, 303–312 (1984).
- 10 Block, B. A., Booth, D. & Carey, F. G. Direct Measurement of Swimming Speeds and Depth of Blue Marlin. *J. Exp. Biol.* **166**, 267–284 (1992).
- 11 Bonner, J. T. *Size and Cycle: An Essay on the Structure of Biology* . (Princeton University Press, 2015).

- 12 Capainolo, P. & Butler, C. A. *How Fast Can A Falcon Dive?: Fascinating Answers to Questions about Birds of Prey*. (Rutgers University Press, 2010).
- 13 Casas, J., Steinmann, T. & Dangles, O. The Aerodynamic Signature of Running Spiders. *PLoS ONE* **3**, e2116 (2008).
- 14 Catry, P., Phillips, R. A. & Croxall, J. P. Sustained fast travel by a gray-headed albatross (*Thalassarche chrysostoma*) riding an antarctic storm. *The Auk* **121**, 1208–1213 (2004).
- 15 Chambers, C. L. *et al.* Roosts and home ranges of spotted bats (*Euderma maculatum*) in northern Arizona. *Can. J. Zool.* **89**, 1256–1267 (2011).
- 16 Christiansen, P. Locomotion in terrestrial mammals: the influence of body mass, limb length and bone proportions on speed. *Zool. J. Linn. Soc.* **136**, 685–714 (2002).
- 17 Clark, C. J. & Dudley, R. Flight costs of long, sexually selected tails in hummingbirds. *Proc. R. Soc. Lond. B Biol. Sci.* rspb.2009.0090 (2009). doi:10.1098/rspb.2009.0090
- 18 Clemente, C. J., Thompson, G. G. & Withers, P. C. Evolutionary relationships of sprint speed in Australian varanid lizards. *J. Zool.* **278**, 270–280 (2009).
- 19 Clements, A. N. The sources of energy for flight in mosquitoes. *J. Exp. Biol.* **32**, 547–554 (1955).
- 20 Collett, T. S. & Land, M. F. How hoverflies compute interception courses. *J. Comp. Physiol.* **125**, 191–204 (1978).
- 21 Combes, S. A. & Dudley, R. Turbulence-driven instabilities limit insect flight performance. *Proc. Natl. Acad. Sci.* **106**, 9105–9108 (2009).
- 22 Corbett, R. J. M., Chambers, C. L. & Herder, M. J. Roosts and activity areas of *Nyctinomops macrotis* in northern Arizona. *Acta Chiropterologica* **10**, 323–329 (2008).
- 23 Cottam, C., Williams, C. S. & Sooter, C. A. Flight and Running Speeds of Birds. *Wilson Bull.* **54**, 121–131 (1942).
- 24 Dangles, O., Ory, N., Steinmann, T., Christides, J.-P. & Casas, J. Spider's attack versus cricket's escape: velocity modes determine success. *Anim. Behav.* **72**, 603–610 (2006).
- 25 David, C. T. The relationship between body angle and flight speed in free-flying *Drosophila*. *Physiol. Entomol.* **3**, 191–195 (1978).
- 26 Davis, R. B., Herreid, C. F. & Short, H. L. Mexican Free-Tailed Bats in Texas. *Ecol. Monogr.* **32**, 311–346 (1962).
- 27 de Albuquerque, R. L., Bonine, K. E. & Garland Jr, T. Speed and endurance do not trade off in phrynosomatid lizards. *Physiol. Biochem. Zool.* **88**, 634–647 (2015).

- 28 Dijkstra, K.-D. B. & Lewington, R. *Field Guide to the Dragonflies of Britain and Europe: Including western Turkey and north-western Africa*. (British Wildlife Publishing Dorset, 2006).
- 29 Dudley, R. *The Biomechanics of Insect Flight: Form, Function, Evolution*. (Princeton University Press, 2002).
- 30 Dunning, J. B., JR. *CRC Handbook of Avian Body Masses*. (CRC Press Inc, 2007).
- 31 Ely, C. R. *et al.* Migration behavior of tundra swans from the Yukon-Kuskokwim Delta, Alaska. *Wilson Bull.* 679–692 (1997).
- 32 Forsythe, T. G. Locomotion in ground beetles (Coleoptera Carabidae): an interpretation of leg structure in functional terms. *J. Zool.* **200**, 493–507 (1983).
- 33 Full, R. J. & Tu, M. S. Mechanics of a rapid running insect: two-, four- and six-legged locomotion. *J. Exp. Biol.* **156**, 215–231 (1991).
- 34 Garland, T. The relation between maximal running speed and body mass in terrestrial mammals. *J. Zool.* **199**, 157–170 (1983).
- 35 Gilbert, C. Visual control of cursorial prey pursuit by tiger beetles (Cicindelidae). *J. Comp. Physiol. A* **181**, 217–230 (1997).
- 36 Gillies, M. T. & Wilkes, T. J. Field experiments with a wind tunnel on the flight speed of some West African mosquitoes (Diptera: Culicidae). *Bull. Entomol. Res.* **71**, 65–70 (1981).
- 37 Gorb, S., Gorb, E. & Kastner, V. Scale effects on the attachment pads and friction forces in syrphid flies (Diptera, Syrphidae). *J. Exp. Biol.* **204**, 1421–1431 (2001).
- 38 Gorb, S. N. & Barth, F. G. Locomotor behavior during prey-capture of a fishing spider, *Dolomedes plantarius* (Araneae: Araneidae): Galloping and stopping. *J. Arachnol.* 89–93 (1994).
- 39 Griffin, L., Rees, E. & Hughes, B. Migration routes of Whooper Swans and geese in relation to wind farm footprints: Final report. *Slimbr. Wildfowl Wetl. Trust WWT* (2011).
- 40 Harkness, R. D. & Wehner, R. *Cataglyphis*. *Endeavour* **1**, 115–121 (1977).
- 41 Hedrick, T. L., Usherwood, J. R. & Biewener, A. A. Wing inertia and whole-body acceleration: an analysis of instantaneous aerodynamic force production in cockatiels (*Nymphicus hollandicus*) flying across a range of speeds. *J. Exp. Biol.* **207**, 1689–1702 (2004).
- 42 Heinrichs, E. A. & others. *Biology and management of rice insects*. (John Wiley & Sons, 1994).
- 43 Hoyo, J. D. & Bateman, R. *Handbook of the Birds of the World, Volume 3*. (Lynx Edicions, 1996).
- 44 Iriarte-Díaz, J. Differential scaling of locomotor performance in small and large terrestrial mammals. *J. Exp. Biol.* **205**, 2897–2908 (2002).

- 45 Kamoun, S. & Hogenhout, S. A. Flightlessness and Rapid Terrestrial Locomotion in Tiger Beetles of the *Cicindela* L. Subgenus *Rivacindela* van Nidek from Saline Habitats of Australia (Coleoptera: Cicindelidae). *Coleopt. Bull.* **50**, 221–230 (1996).
- 46 Kear, J. *Ducks, Geese and Swans: General chapters, species accounts (Anhima to Salvadorina)*. (Oxford University Press, 2005).
- 47 Kikuchi, Y. & Fukatsu, T. Live imaging of symbiosis: spatiotemporal infection dynamics of a GFP-labelled *Burkholderia* symbiont in the bean bug *Riptortus pedestris*. *Mol. Ecol.* **23**, 1445–1456 (2014).
- 48 Kils, U. *The swimming behavior, swimming performance and energy balance of Antarctic krill, Euphausia superba*. (SCAR and SCOR, Scott Polar Research Institute, 1981).
- 49 Kooyman, G. L. *et al.* Heart rates and swim speeds of emperor penguins diving under sea ice. *J. Exp. Biol.* **165**, 161–180 (1992).
- 50 Laming, S. R., Jenkins, S. R. & McCarthy, I. D. Repeatability of escape response performance in the queen scallop, *Aequipecten opercularis*. *J. Exp. Biol.* **216**, 3264–3272 (2013).
- 51 Li, X., Ma, L., Sun, L. & Zhu, C. Biotic characteristics in the deltamethrin-susceptible and resistant strains of *Culex pipiens pallens* (Diptera: Culicidae) in China. *Appl. Entomol. Zool.* **37**, 305–308 (2002).
- 52 Marden, J. H., Wolf, M. R. & Weber, K. E. Aerial performance of *Drosophila melanogaster* from populations selected for upwind flight ability. *J. Exp. Biol.* **200**, 2747–2755 (1997).
- 53 Marsh, A. C. Microclimatic factors influencing foraging patterns and success of the thermophilic desert ant, *Ocymyrmex barbiger*. *Insectes Sociaux* **32**, 286–296 (1985).
- 54 McGinley, R. H., Prenter, J. & Taylor, P. W. Whole-organism performance in a jumping spider, *Servaea incana* (Araneae: Salticidae): links with morphology and between performance traits. *Biol. J. Linn. Soc.* **110**, 644–657 (2013).
- 55 McKibben, G. H., Willers, J. L., Smith, J. W. & Wagner, T. L. Stochastic model for studying boll weevil dispersal. *Environ. Entomol.* **20**, 1327–1332 (1991).
- 56 Myhrvold, N. P. *et al.* An amniote life-history database to perform comparative analyses with birds, mammals, and reptiles. *Ecology* **96**, 3109–3109 (2015).
- 57 Nelson, M. K. & Formanowicz, D. R. Relationship between escape speed and flight distance in a wolf spider, *Hogna carolinensis* (Walckenaer 1805). *J. Arachnol.* **33**, 153–158 (2005).
- 58 Noad, M. J. & Cato, D. H. Swimming Speeds of Singing and Non-Singing Humpback Whales During Migration. *Mar. Mammal Sci.* **23**, 481–495 (2007).

- 59 Nowak, R. M. *Walker's Mammals of the World* . **1**, (JHU Press, 1999).
- 60 O'Donnell, C. F. J. Home range and use of space by *Chalinolobus tuberculatus* , a temperate rainforest bat from New Zealand. *J. Zool.* **253**, 253–264 (2001).
- 61 O'DOR, R. & Webber, D. M. Invertebrate athletes: trade-offs between transport efficiency and power density in cephalopod evolution. *J. Exp. Biol.* **160**, 93–112 (1991).
- 62 Patterson, A. P. & Hardin, J. W. Flight speeds of five species of vespertilionid bats. *J. Mammal.* 152–153 (1969).
- 63 Pistorius, P. A. *et al.* Distribution, movement, and estimated population size of killer whales at Marion Island, December 2000. *South Afr. J. Wildl. Res.* **32**, p–86 (2002).
- 64 Pitnick, S., Markow, T. A. & Spicer, G. S. Delayed male maturity is a cost of producing large sperm in *Drosophila* . *Proc. Natl. Acad. Sci.* **92**, 10614–10618 (1995).
- 65 Prenter, J., Pérez-Staples, D. & Taylor, P. W. Functional relations between locomotor performance traits in spiders and implications for evolutionary hypotheses. *BMC Res. Notes* **3**, 306 (2010).
- 66 Pruitt, J. N. & Husak, J. F. Context-dependent running speed in funnel-web spiders from divergent populations. *Funct. Ecol.* **24**, 165–171 (2010).
- 67 Roberts, M. J. & others. *Spiders of Britain & Northern Europe* . (HarperCollins Publishers, 1995).
- 68 Rohr, J. J., Fish, F. E. & Gilpatrick, J. W. Maximum swim speeds of captive and free-ranging delphinids: Critical analysis of extraordinary performance. *Mar. Mammal Sci.* **18**, 1–19 (2002).
- 69 Rubin, S., Young, M. H.-Y., Wright, J. C., Whitaker, D. L. & Ahn, A. N. Exceptional running and turning performance in a mite. *J. Exp. Biol.* **219**, 676–685 (2016).
- 70 Ruppell, G. Kinematic analysis of symmetrical flight manoeuvres of Odonata. *J. Exp. Biol.* **144**, 13–42 (1989).
- 71 Sachs, G. *et al.* Flying at no mechanical energy cost: disclosing the secret of wandering albatrosses. *PloS One* **7**, e41449 (2012).
- 72 Saleuddin, A. S. M. & Wilbur, K. M. *The Mollusca: Physiology* . **5**, (Academic Press, 2012).
- 73 Schmidt, W. *Reptiles & Amphibians of Southern Africa* . (Struik, 2006).
- 74 Spagna, J. C., Valdivia, E. A. & Mohan, V. Gait characteristics of two fast-running spider species (*Hololena adnexa* and *Hololena curta*), including an aerial phase (Araneae: Agelenidae). *J. Arachnol.* **39**, 84–91 (2011).

- 75 Stevenson, R., Corbo, K., Baca, L. & Le, Q. Cage size and flight speed of the tobacco hawkmoth *Manduca sexta* . *J. Exp. Biol.* **198**, 1665–1672 (1995).
- 76 Ting, L. H., Blickhan, R. & Full, R. J. Dynamic and static stability in hexapedal runners. *J. Exp. Biol.* **197**, 251–269 (1994).
- 77 Tsunoda, T. & Moriya, S. Measurement of flight speed and estimation of flight distance of the bean bug, *Riptortus pedestris* (Fabricius)(Heteroptera: Alydidae) and the rice bug, *Leptocorisa chinensis* Dallas (Heteroptera: Alydidae) with a speed sensor and flight mills. *Appl. Entomol. Zool.* **43**, 451–456 (2008).
- 78 Tudorache, C., Viaene, P., Blust, R., Vereecken, H. & De Boeck, G. A comparison of swimming capacity and energy use in seven European freshwater fish species. *Ecol. Freshw. Fish* **17**, 284–291 (2008).
- 79 Uchiyama, J. H. & Boggs, C. H. Length-weight relationships of dolphinfish, *Coryphaena hippurus* , and wahoo, *Acanthocybium solandri* : seasonal effects of spawning and possible migration in the central North Pacific. *Mar. Fish. Rev.* **68**, 19–29 (2006).
- 80 Van Damme, R. & Vanhooydonck, B. Origins of interspecific variation in lizard sprint capacity. *Funct. Ecol.* **15**, 186–202 (2001).
- 81 Vogel, S. Flight in *Drosophila* I. Flight performance of tethered flies. *J. Exp. Biol.* **44**, 567–578 (1966).
- 82 Walters, V. & Fierstine, H. L. Measurements of swimming speeds of yellowfin tuna and wahoo. *Biol. Sci.* **2** (1964).
- 83 Wehner, R., Fukushi, T. & Isler, K. On being small: brain allometry in ants. *Brain. Behav. Evol.* **69**, 220–228 (2007).
- 84 Whitehead, H. *Sperm Whales: Social Evolution in the Ocean* . (University of Chicago Press, 2003).
- 85 Williams, T. M. *et al.* Running energetics of the North American river otter: do short legs necessarily reduce efficiency on land? *Comp. Biochem. Physiol. A. Mol. Integr. Physiol.* **133**, 203–212 (2002).
- 86 Willmott, A. P. & Ellington, C. P. The mechanics of flight in the hawkmoth *Manduca sexta* . I. Kinematics of hovering and forward flight. *J. Exp. Biol.* **200**, 2705–2722 (1997).
- 87 Wilson, D. S. Prudent Predation: A Field Study Involving Three Species of Tiger Beetles. *Oikos* **31**, 128–136 (1978).
- 88 Winter, Y. Flight speed and body mass of nectar-feeding bats (Glossophaginae) during foraging. *J. Exp. Biol.* **202**, 1917–1930 (1999).
- 89 Wu, G. C., Wright, J. C., Whitaker, D. L. & Ahn, A. N. Kinematic evidence for superfast locomotory muscle in two species of teneriffiid mites. *J. Exp. Biol.* **213**, 2551–2556 (2010).
- 90 Yin, M. C. & Blaxter, J. H. S. Escape speeds of marine fish larvae during early development and starvation. *Mar. Biol.* **96**, 459–468 (1987).

non-peer reviewed

- 91 Gierak, R. 2013. "*Euphausia superba* " (On-line), Animal Diversity Web. http://animaldiversity.org/accounts/Euphausia_superba/
- 92 Glyshaw, P. and E. Wason 2013. "*Anopheles quadrimaculatus* "(On-line), Animal Diversity Web. http://animaldiversity.org/accounts/Anopheles_quadrimaculatus/
- 93 Ivory, A. 2002. "*Aquila chrysaetos* " (On-line), Animal Diversity Web. http://animaldiversity.org/accounts/Aquila_chrysaetos/
- 94 Thompson, B. 2001. "*Anthonomus grandis* " (On-line), Animal Diversity Web. http://animaldiversity.org/accounts/Anthonomus_grandis/
- 95 Tung, L. 2003. "*Makaira nigricans* " (On-line), Animal Diversity Web. http://animaldiversity.org/accounts/Makaira_nigricans/
- 96 www.allaboutbirds.org/guide/Peregrine_Falcon/lifehistory
- 97 www.nationalgeographic.com/animals/mammals/c/california-sea-lion/
- 98 www.howfastcanarun.com/how-fast-can-a-pig-run.html
- 99 www.livescience.com/32772-what-animal-is-the-fastest-swimmer.html
- 100 www.oceanwide-expeditions.com/to-do/wildlife/ringed-seal-1
- 101 www.speedofanimals.com
- 102 www.theanimalfiles.com/mammals/hoofed_mammals/chital.html
- 103 www.wikipedia.org/wiki/Shortfin_mako_shark