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 ranges[1] and meta-communities[2], movement also profoundly affects the ability of animals to cope with changes in land use and in climate[3]. Additionally, movement determines encounter rates and thus the strength of species interactions[4], which is an important factor influencing ecosystem stability[5]. 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 $v_{max(theor)}$ of animals with body mass M:

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

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

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

The acceleration constant k describes how fast an animal reaches $v_{max(theor)}$. 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:

$$k = cM^{d-1} \tag{3}$$

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,

[1]EcoNetLab, German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig 04103, Germany. [2]EcoNetLab, Friedrich Schiller University Jena, Dornburger Strasse 159, 07743 Jena, Germany. [3]Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT 06511, USA. [4]Department of Life Sciences, Imperial College London, Silwood Park, Ascot SL5 7QN, UK. *e-mail: myriam.hirt@idiv.de
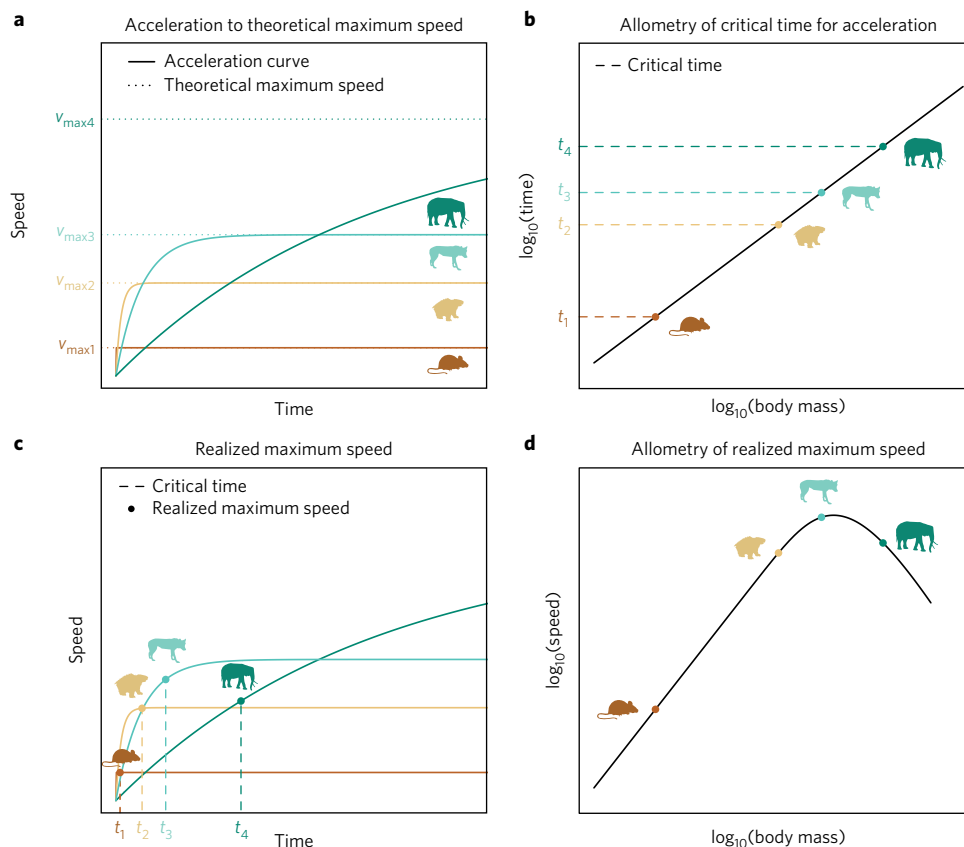
Figure 1 | Concept of time-dependent and mass-dependent realized maximum speed of animals. a, Acceleration of animals follows a saturation curve (solid lines) approaching the theoretical maximum speed (dotted lines) depending on body mass (colour code). **b**, The time available for acceleration increases 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:

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

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

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

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
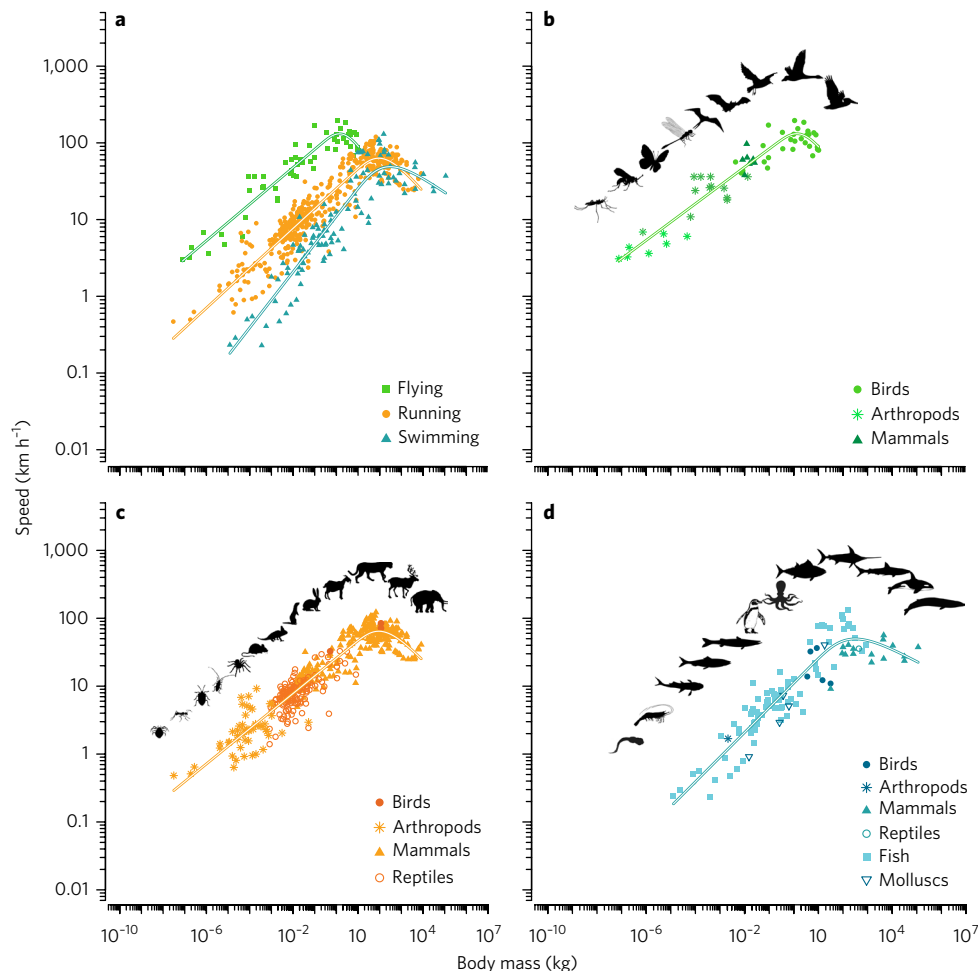
1117

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 air[30] (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 (ΔBIC $= 27.37$). 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
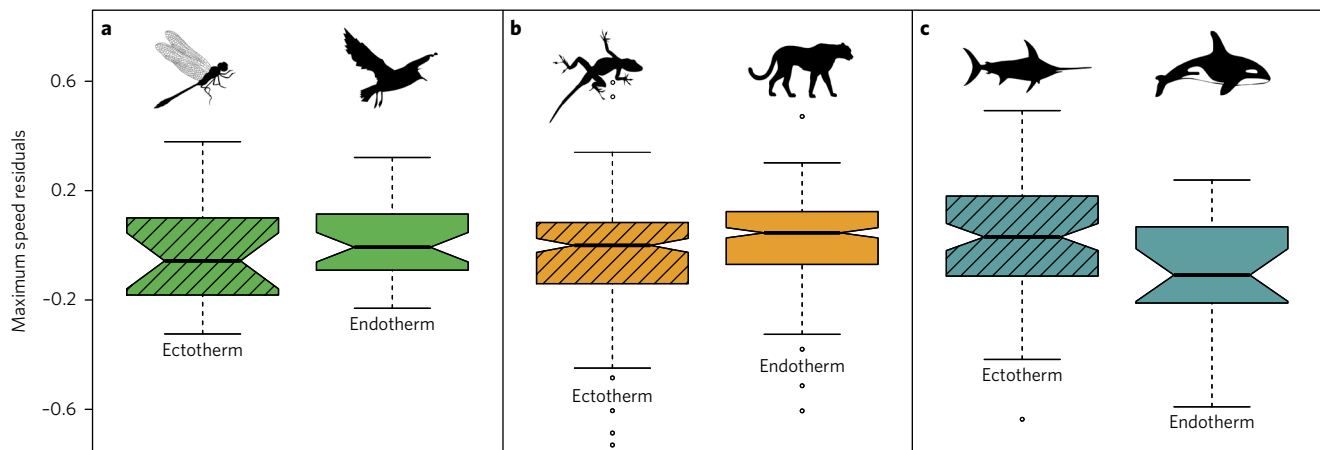
Figure 3 | Effect of thermoregulation on the maximum speed of animals. These are the residuals of the relationship in Fig. 2. **a,b**, In flying (**a**) and running (**b**) animals, endotherms are generally faster than ectotherms. **c**, In swimming animals, this effect is reversed, with ectotherms being 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 nature[31]. 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 transport[32]. 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 temperature[32]. 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 constraints[13], 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 speed[17]. 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 birds[34] 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 runner[37]. 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 temperature[40]. 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				
Dromaius (extant)	27.2	40.92 (38.58–43.40)	47.88	57.62 (47.65–60.91)
Struthio (extant)	65.3	49.33 (46.27–52.59)	55.44	62.75 (46.71–66.03)
Patagornis (extinct)	45	45.56 (42.83–48.46)	50.40	61.34 (47.39–64.68)
Bipedal dinosaurs				
Velociraptor	20	38.32 (36.19–40.58)	38.88	54.56 (46.89–57.82)
Allosaurus	1,400	94.87 (87.09–103.34)	33.84	40.78 (28.93–44.83)
Tyrannosaurus	6,000	129.41 (117.47–142.57)	28.8	27.05 (17.84–31.52)
Quadrupedal dinosaurs				
Triceratops	8,478	139.32 (126.11–153.91)	26.4	24.36 (15.70–28.83)
Apatosaurus	27,869	179.59 (161.01–200.31)	12.3	16.75 (9.77–21.09)
Brachiosaurus	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 ranges[1,41] and day ranges[42] 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 mass[43]. 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 nd 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].
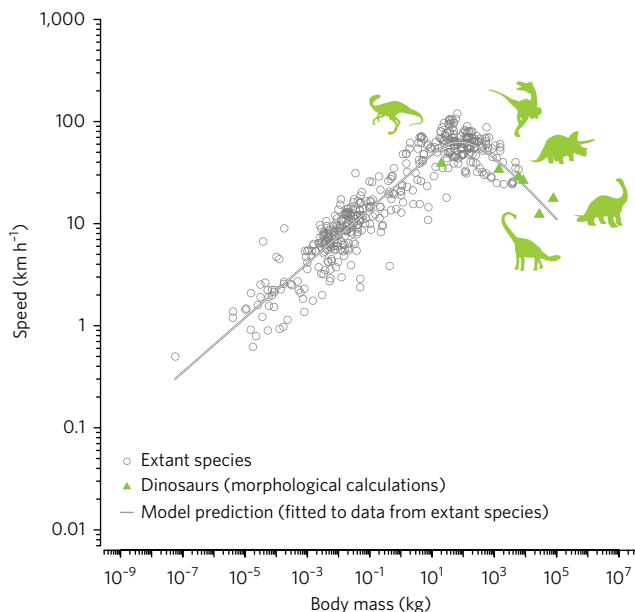
Figure 4 | Predicting the maximum speed of extinct species with the time-dependent model. The model prediction (grey line) is fitted to data of extant species (grey circles) and extended to higher body masses. Speed data for dinosaurs (green triangles) come from detailed morphological model calculations (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 estimates[45]. 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.

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. & Hoye, 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, Rm, 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., Cowlishaw, 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

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

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]

---

[1]EcoNetLab, German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig 04103, Germany. [2]EcoNetLab, Friedrich Schiller University Jena, Dornburger Strasse 159, 07743 Jena, Germany. [3]Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT 06511, USA. [4]Department 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

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

Models	Δ BIC		
	flying	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	reference power law	morphological model	time-dependent model
Dromaius	(1)	*	(1)	+
Struthio	(1)	*	(1)	+
Patagornis	(2)	*	(2)	+
Velociraptor	(1)	*	(1)	+
Allosaurus	(1)	*	(1)	+
Tyrannosaurus	(1)	*	(1)	+
Triceratops	(3)	*	(3)	+
Apatosaurus	(3)	*	(3)	+
Brachiosaurus	(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
Aeshna cyanea	arthropod	flying	ectotherm	4.22E-04	*28*	36	*70*	carnivore
Anax junius	arthropod	flying	ectotherm	4.50E-04	*28*	27	*70*	carnivore
Anax parthenope julius	arthropod	flying	ectotherm	3.90E-04	*28*	25.92	*4*	carnivore
Anax sp.	arthropod	flying	ectotherm	0.0138	*11*	36	*11*	carnivore
Anopheles ziemanni	arthropod	flying	ectotherm	5.22E-06	*92*	6.48	*36*	carnivore
Anthonomus grandis	arthropod	flying	ectotherm	6.86E-06	*94*	4.8	*55*	herbivore
Culex pipiens	arthropod	flying	ectotherm	1.30E-06	*51*	3.6	*19*	carnivore
Drosophila hydei	arthropod	flying	ectotherm	1.76E-07	*64*	3.24	*25*	herbivore
Drosophila melanogaster	arthropod	flying	ectotherm	7.47E-07	*11*	6.84	*11*	herbivore
Drosophila melanogaster	arthropod	flying	ectotherm	7.89E-08	*64*	3.06	*52*	herbivore
Drosophila virilis	arthropod	flying	ectotherm	2.05E-07	*64*	4.32	*81*	herbivore
Eristalis sp.	arthropod	flying	ectotherm	9.00E-05	*37*	36	*20*	herbivore
Volucella pellucens	arthropod	flying	ectotherm	1.70E-04	*37*	36	*20*	herbivore
Euglossa imperialis	arthropod	flying	ectotherm	0.0015	*29*	25.56	*21*	herbivore
Leptocorisa chinensis	arthropod	flying	ectotherm	4.73E-05	*42*	6	*77*	herbivore
Manduca sexta	arthropod	flying	ectotherm	0.002	*29*	19.08	*75*	herbivore
Manduca sexta	arthropod	flying	ectotherm	0.002	*29*	18	*86*	herbivore
Riptortus pedestris	arthropod	flying	ectotherm	6.52E-05	*47*	10.8	*77*	herbivore
Tabanus affinis	arthropod	flying	ectotherm	1.01E-04	*11*	23.76	*11*	carnivore
Accipiter striatus	bird	flying	endotherm	0.0965	*30*	64	*12*	carnivore
Anas acuta	bird	flying	endotherm	0.947	*30*	82.08	*11*	omnivore
Anas platyrhynchos	bird	flying	endotherm	1.14	*30*	105	*101*	omnivore
Apus apus	bird	flying	endotherm	0.058	*11*	91.8	*11*	carnivore
Aquila chrysaetos	bird	flying	endotherm	4.2635	*30*	129	*93*	carnivore
Archilochus colubris	bird	flying	endotherm	0.0075	*11*	40.32	*11*	herbivore
Buteo jamaicensis	bird	flying	endotherm	1.11	*30*	195	*101*	carnivore
Calypte anna	bird	flying	endotherm	0.0044	*56*	56.16	*17*	herbivore
Chen caerulescens	bird	flying	endotherm	2.641	*30*	185	*46*	herbivore

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

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

Species	Group	Locomotion	Thermoregulation	Mass	n1	Speed	n2	Diet
Schizocosa ocreata (Size class 3)	arthropod	running	ectotherm	3.11E-05	*24*	2.53	*24*	carnivore
Schizocosa ocreata (Size class 4)	arthropod	running	ectotherm	4.49E-05	*24*	2.64	*24*	carnivore
Schizocosa ocreata (Size class 5)	arthropod	running	ectotherm	5.30E-05	*24*	2.23	*24*	carnivore
Servaea incana	arthropod	running	ectotherm	5.36E-05	*54*	0.9	*54*	carnivore
Varacosa terricola (Size class 1)	arthropod	running	ectotherm	1.76E-04	*24*	2.57	*24*	carnivore
Varacosa terricola (Size class 2)	arthropod	running	ectotherm	2.87E-04	*24*	2.57	*24*	carnivore
Varacosa terricola (Size class 3)	arthropod	running	ectotherm	3.20E-04	*24*	2.50	*24*	carnivore
Varacosa terricola (Size class 4)	arthropod	running	ectotherm	4.87E-04	*24*	2.72	*24*	carnivore
Varacosa terricola (Size class 5)	arthropod	running	ectotherm	5.28E-04	*24*	2.24	*24*	carnivore
Varacosa terricola (Size class 6)	arthropod	running	ectotherm	6.01E-04	*24*	2.11	*24*	carnivore
Varacosa terricola (Size class 7)	arthropod	running	ectotherm	7.17E-04	*24*	1.84	*24*	carnivore
Geococcyx californianus	bird	running	endotherm	0.5	*101*	32	*101*	omnivore
Struthio camelus	bird	running	endotherm	111	*30*	70	*101*	herbivore
Struthio camelus	bird	running	endotherm	111	*30*	82.8	*11*	herbivore
Acinonyx jubatus	mammal	running	endotherm	39	*16*	104.95	*16*	carnivore
Acinonyx jubatus	mammal	running	endotherm	65	*101*	120	*101*	carnivore
Acinonyx jubatus	mammal	running	endotherm	58.8	*44*	106.91	*44*	carnivore
Acinonyx jubatus	mammal	running	endotherm	44.87	*11*	104.4	*11*	carnivore
Aepyceros melampus	mammal	running	endotherm	50	*16*	74.99	*16*	herbivore
Aepyceros melampus	mammal	running	endotherm	50	*34*	47	*34*	herbivore
Aepyceros melampus	mammal	running	endotherm	53.25	*7*	45.68	*7*	herbivore
Alcelaphus buselaphus	mammal	running	endotherm	150	*16*	69.98	*16*	herbivore
Alcelaphus buselaphus	mammal	running	endotherm	170	*34*	80	*34*	herbivore
Alcelaphus buselaphus	mammal	running	endotherm	136	*7*	77.98	*7*	herbivore
Alces alces	mammal	running	endotherm	410.2	*16*	55.98	*16*	herbivore
Alces alces	mammal	running	endotherm	384	*7*	54.55	*7*	herbivore
Ammospermophilus leucurus	mammal	running	endotherm	0.0759	*44*	16.77	*44*	omnivore
Antechinomys laniger	mammal	running	endotherm	0.025	*44*	14.51	*44*	carnivore
Antechinus flavipes	mammal	running	endotherm	0.052	*44*	16.20	*44*	carnivore
Antechinus stuartii	mammal	running	endotherm	0.0315	*44*	17.38	*44*	carnivore
Antidorcas marsupialis	mammal	running	endotherm	21.18	*16*	87.90	*16*	herbivore
Antidorcas marsupialis	mammal	running	endotherm	34	*34*	97	*34*	herbivore
Antidorcas marsupialis	mammal	running	endotherm	34	*7*	94.302	*7*	herbivore

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

Species	Class	Locomotion	Thermoregulation	Mass	Col6	Speed	Col8	Diet
Ceratotherium simum	mammal	running	endotherm	2000	*7*	24.36	*7*	herbivore
Ceratotherium simum	mammal	running	endotherm	1901	*16*	39.99	*16*	herbivore
Ceratotherium simum	mammal	running	endotherm	3000	*34*	25	*34*	herbivore
Cercartetus concinnus	mammal	running	endotherm	0.015	*44*	4.84	*44*	carnivore
Cervus canadensis	mammal	running	endotherm	382	*101*	72.4	*101*	herbivore
Cervus elaphus	mammal	running	endotherm	84.92	*16*	71.94	*16*	herbivore
Chaetodipus baileyi	mammal	running	endotherm	0.0391	*44*	12.09	*44*	herbivore
Chaetodipus fallax	mammal	running	endotherm	0.018	*44*	12.45	*44*	herbivore
Connochaetes gnou	mammal	running	endotherm	157	*16*	79.98	*16*	herbivore
Connochaetes gnou	mammal	running	endotherm	250	*101*	64	*101*	herbivore
Connochaetes gnou	mammal	running	endotherm	300	*34*	90	*34*	herbivore
Connochaetes gnou	mammal	running	endotherm	132.25	*56*	62.18	*7*	herbivore
Connochaetes gnou	mammal	running	endotherm	132.25	*56*	69.97	*7*	herbivore
Connochaetes taurinus	mammal	running	endotherm	180	*34*	79.98	*16*	herbivore
Crocuta crocuta	mammal	running	endotherm	65.01	*16*	59.98	*16*	carnivore
Crocuta crocuta	mammal	running	endotherm	50	*101*	64	*101*	carnivore
Crocuta crocuta	mammal	running	endotherm	52	*44*	62.99	*44*	carnivore
Dama dama	mammal	running	endotherm	45	*16*	65.01	*16*	herbivore
Dama dama	mammal	running	endotherm	55	*7*	63.40	*7*	herbivore
Damaliscus dorcas	mammal	running	endotherm	43.45	*16*	69.98	*16*	herbivore
Damaliscus hunteri	mammal	running	endotherm	158.85	*16*	69.98	*16*	herbivore
Damaliscus lunatus	mammal	running	endotherm	125.89	*16*	69.98	*16*	herbivore
Damaliscus lunatus	mammal	running	endotherm	130	*7*	68.24	*7*	herbivore
Dasyuroides byrnei	mammal	running	endotherm	0.12	*44*	25.66	*44*	carnivore
Diceros bicornis	mammal	running	endotherm	875	*16*	44.98	*16*	herbivore
Diceros bicornis	mammal	running	endotherm	1200	*7*	43.80	*7*	herbivore
Dipodomys deserti	mammal	running	endotherm	0.0976	*44*	14.63	*44*	herbivore
Dipodomys merriami	mammal	running	endotherm	0.035	*44*	31.22	*44*	herbivore
Dipodomys microps	mammal	running	endotherm	0.056	*44*	20.43	*44*	herbivore
Dipodomys ordii	mammal	running	endotherm	0.0478	*44*	13.66	*44*	herbivore
Elephas maximus	mammal	running	endotherm	4000	*34*	26	*34*	herbivore
Elephas maximus	mammal	running	endotherm	4000	*7*	25.28	*7*	herbivore
Equus asinus	mammal	running	endotherm	165.2	*16*	54.95	*16*	herbivore

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

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

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

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

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

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

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

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

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

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

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

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

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

terrestrial arthropods   Jurkschat L. Allometric scaling relationships in the morphology of temperate and tropical arthropods. Master's Thesis. Univ. of Göttingen (2015)

others   Peters, R. H. *The ecological implications of body size* . **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   Rüppell, 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