

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

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**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.**

**M**ovement 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<sup>1</sup> and meta-communities<sup>2</sup>, movement also profoundly affects the ability of animals to cope with changes in land use and in climate<sup>3</sup>. Additionally, movement determines encounter rates and thus the strength of species interactions<sup>4</sup>, which is an important factor influencing ecosystem stability<sup>5</sup>. Accordingly, a generalized and predictive understanding of animal movement is crucial<sup>6,7</sup>.

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<sup>8–10</sup>. However, scientists have always struggled with the fact that, in running animals, the largest are not the fastest<sup>11–14</sup>. 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<sup>11–13,15,16</sup>. Although biomechanical and morphological models have been tailored to explain this within taxonomic groups<sup>14,16–18</sup>, 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<sup>8,10</sup>, we start with a power-law scaling of theoretical maximum speed  $v_{\max(\text{theor})}$  of animals with body mass  $M$ :

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

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

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

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

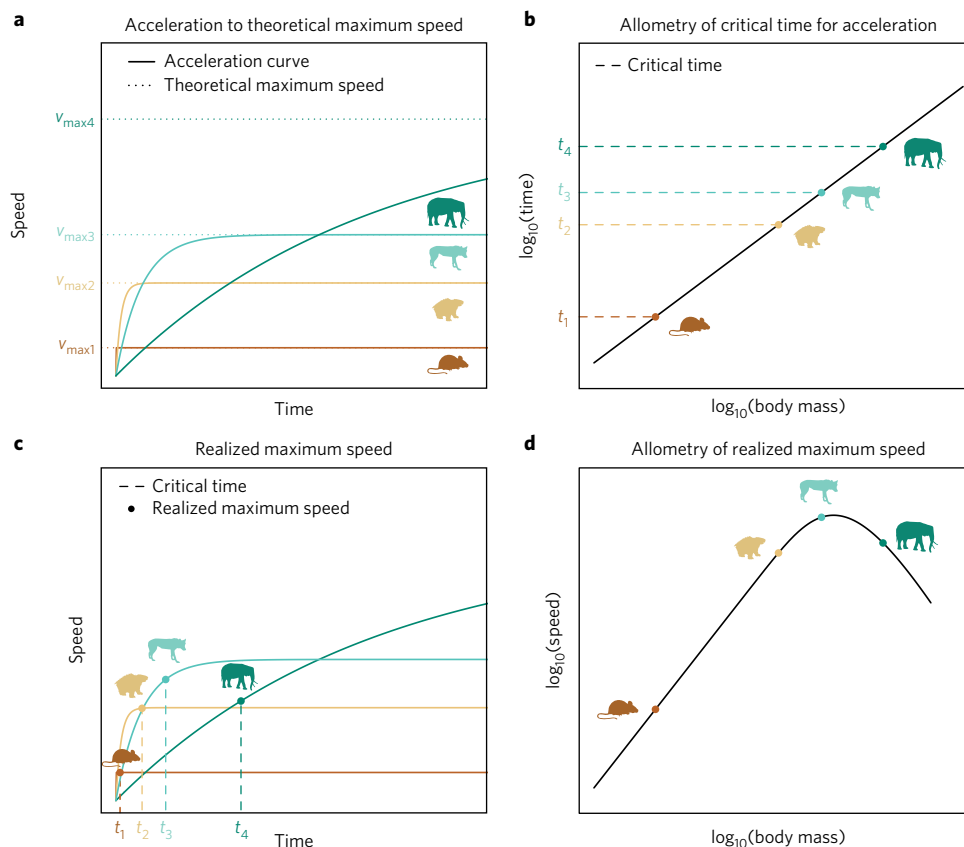
$$k = cM^{d-1} \quad (3)$$

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

Whereas prolonged high speeds are related to the maximum aerobic metabolism, maximum burst speeds are linked to anaerobic capacity<sup>24,25</sup>. 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,

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**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  $\tau$  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,  $\tau$  should follow a power law:

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

where the allometric exponent  $g$  should fall in the range 0.76 to 1.27 documented for the allometric scaling of muscle tissue mass<sup>26–29</sup>. 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  $\tau$  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  $\tau$  (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  $\tau$ , after which the energy available for acceleration is depleted, the animal reaches its realized maximum

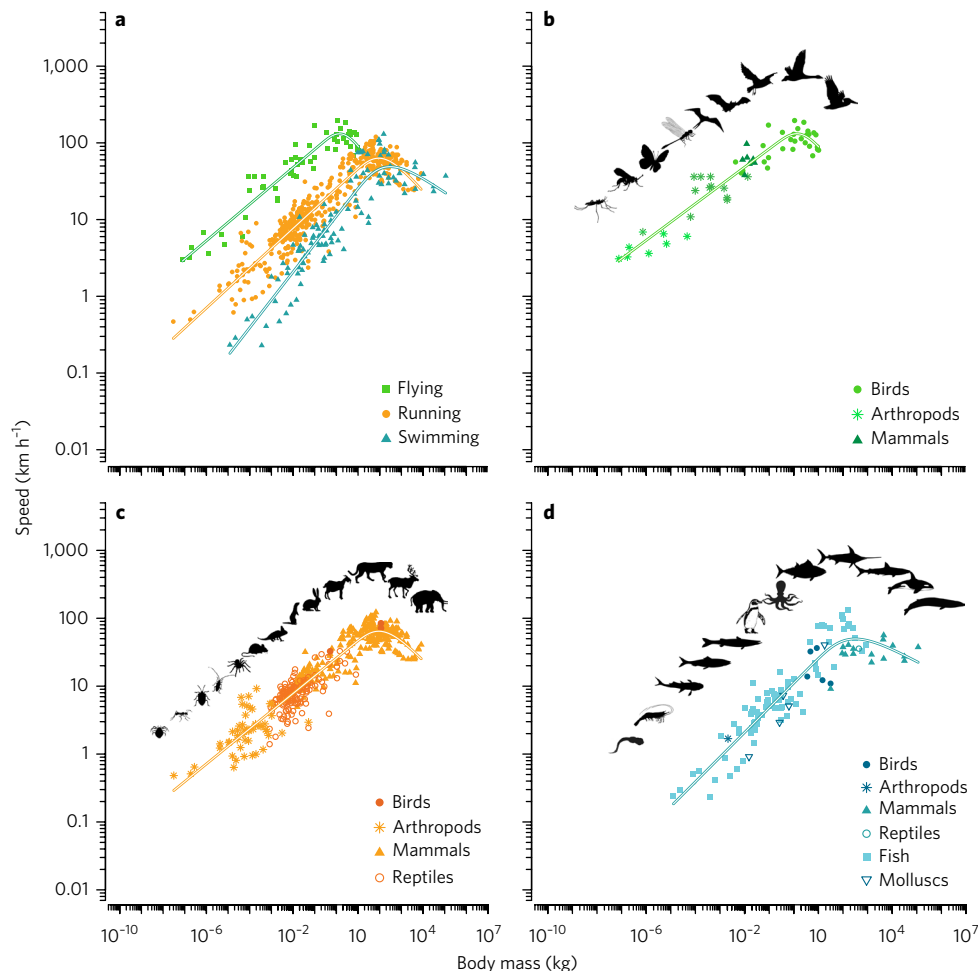
speed  $v_{\max}$  (points in Fig. 1c), which may be lower than the theoretical maximum speed (Fig. 1a, dotted lines). Combining equations (1)–(4) with  $t = \tau$  yields  $v_{\max} = aM^b(1 - e^{-cfM^{d-1+g}})$  which simplifies to

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

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

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

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

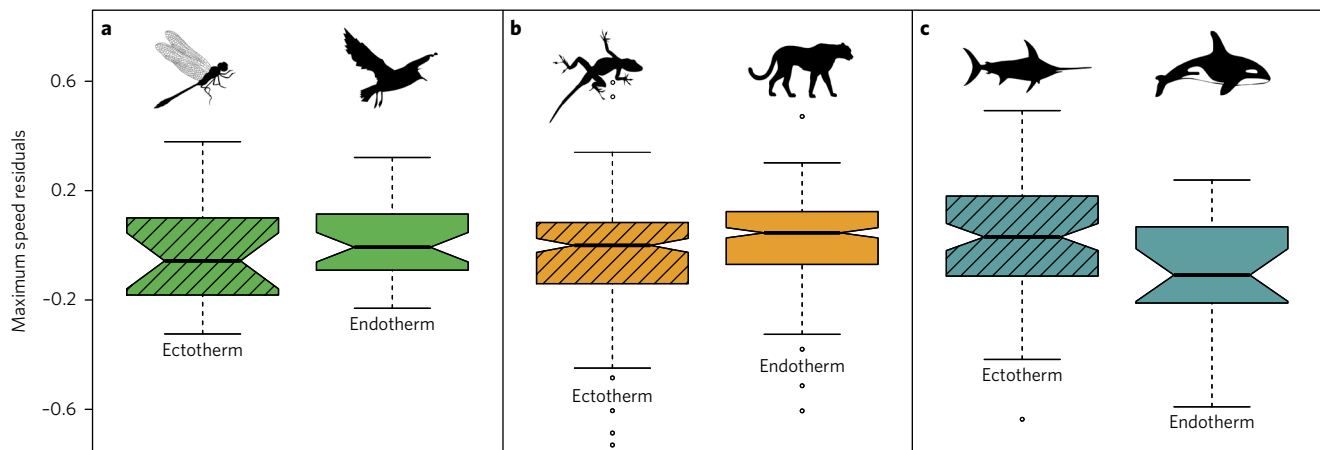


**Figure 2 | Empirical data and time-dependent model fit for the allometric scaling of maximum speed.** **a**, Comparison of scaling for the different locomotion modes (flying, running, swimming). **b–d**, Taxonomic differences are illustrated separately for flying (**b**;  $n=55$ ), running (**c**;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

from  $3 \times 10^{-8}$  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<sup>30</sup> (in which both flying and running animals move). Small aquatic animals are slower than running animals of the same body mass, whereas larger species approach a similar speed to that of their running equivalents. This implies that in water, body mass brings a greater benefit in gaining speed. The second exponent is lower for flying animals ( $i=-0.72$ ) than for running ( $i=-0.6$ ) and swimming ones ( $i=-0.56$ ). Future research will need to disentangle the relative importance of anaerobic and musculoskeletal constraints on movement speed by measuring muscle force, muscle mass, body mass and maximum acceleration for the same species to narrow down this large range of possible exponents. Furthermore, this may allow us to address the systematic differences in the exponent  $i$  between the locomotion modes as well as potential morphological side effects

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

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



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

in nature<sup>31</sup>. 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  $2.4 \times 10^5$  times higher costs of transport<sup>32</sup>. 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<sup>32</sup>. 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<sup>13</sup>, thus implying that speed scaling depends on body-mass range<sup>11,12</sup>. Others have invoked morphology, locomotion energetics and biomechanics<sup>10–13,15,17,18</sup> 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<sup>17,18,33</sup>. 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<sup>17</sup>. 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<sup>34</sup> and dinosaurs<sup>35,36</sup> that roamed past ecosystems. The benchmark of speed predictions is set by detailed morphological models<sup>35,36</sup>. 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<sup>37</sup>. 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)<sup>38,39</sup>, it is not surprising that some variables of movement speed and acceleration also increase with temperature<sup>40</sup>. 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 <sup>-1</sup> )		
		Power law (95% CI)	Morphological models	Time-dependent model (95% CI)
Flightless birds				
<i>Dromaius</i> (extant)	27.2	40.92 (38.58–43.40)	47.88	57.62 (47.65–60.91)
<i>Struthio</i> (extant)	65.3	49.33 (46.27–52.59)	55.44	62.75 (46.71–66.03)
<i>Patagornis</i> (extinct)	45	45.56 (42.83–48.46)	50.40	61.34 (47.39–64.68)
Bipedal dinosaurs				
<i>Velociraptor</i>	20	38.32 (36.19–40.58)	38.88	54.56 (46.89–57.82)
<i>Allosaurus</i>	1,400	94.87 (87.09–103.34)	33.84	40.78 (28.93–44.83)
<i>Tyrannosaurus</i>	6,000	129.41 (117.47–142.57)	28.8	27.05 (17.84–31.52)
Quadrupedal dinosaurs				
<i>Triceratops</i>	8,478	139.32 (126.11–153.91)	26.4	24.36 (15.70–28.83)
<i>Apatosaurus</i>	27,869	179.59 (161.01–200.31)	12.3	16.75 (9.77–21.09)
<i>Brachiosaurus</i>	78,258	223.85 (199.00–251.80)	17.6	11.99 (6.39–16.04)

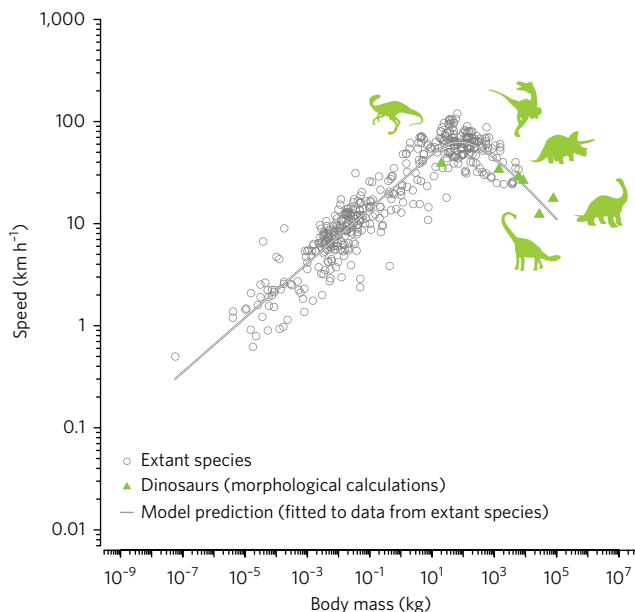
Model predictions of a simple power law, morphological models and our time-dependent maximum-speed model are compared (references in Supplementary Table 5). Confidence intervals (95% CI) are given for the power law and time-dependent model.

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

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

a power-law relationship with body mass, large and small animals would use a higher proportion of their maximum speed during travel than intermediately sized animals. This would also affect different measurements of animal space use as well as migration and dispersal distances. Although home ranges<sup>41</sup> and day ranges<sup>42</sup> 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<sup>43</sup>. Our new results call for mechanistic analyses of how the hump-shaped scaling pattern of maximum speed could potentially affect other movement parameters.

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



**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)<sup>44</sup>. 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<sup>45</sup>. 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.

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**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**

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