

14 **Abstract**

15 Speed is the fundamental constraint on animal movement, yet there is no general consensus on the
16 determinants of maximum speed itself. Here, we provide a universal scaling model of maximum
17 speed with body mass, which holds across locomotion modes, ecosystem types and taxonomic
18 groups. In contrast to traditional power-law scaling, we predict a hump-shaped relationship due to
19 a finite acceleration time for animals. This model is strongly supported by extensive empirical data
20 (470 species with body masses ranging from 5.7×10^{-8} to 108,000 kg) from terrestrial as well as
21 aquatic ecosystems. Our approach offers a novel concept of what determines the upper limit of
22 animal movement, thus enabling a better understanding of realized movement patterns in nature
23 and their multifold ecological consequences.

24

25 **Main text**

26 The movement of animals and its consequences for ecosystem functioning have long fascinated
27 humans and triggered enormous research^{1,2}. Nevertheless, a generalized understanding of what
28 determines variation in movement across species and environments is still lacking. This is
29 particularly important as movement is one of the most fundamental processes of life: the individual
30 survival of mobile organisms depends on their ability to reach resources and mating partners,
31 escape predators, and switch between habitat patches or breeding and wintering grounds.
32 Moreover, by creating and sustaining individual home ranges³ and meta-communities⁴, movement
33 also profoundly affects the ability of animals to cope with land-use and climate changes⁵.
34 Additionally, movement determines encounter rates and thus the strength of species interactions⁶,
35 which is an important factor influencing ecosystem stability⁷. Thus, a generalized and predictive
36 understanding of animal movement is crucial.

37 Maximum speed is the fundamental constraint of movement. The realized movement depends on
38 ecological factors such as landscape structure, habitat quality, or sociality, but the range within
39 which this realized movement occurs meets its upper limit at maximum movement speed. Similar
40 to many physiological and ecological parameters, movement speed of animals is often thought to
41 follow a power-law relationship with body mass⁸⁻¹⁰. However, scientists have always struggled
42 with the fact that in running animals the largest are not the fastest. In nature, the fastest animals
43 such as cheetahs or marlins are of intermediate size indicating that a hump-shaped pattern may be
44 more realistic. There have been numerous attempts to describe this phenomenon¹¹⁻¹⁵, but a
45 universal mechanistic model explaining this relationship is still lacking. Here, we fill this void by
46 a novel maximum speed model based on the concept that animals are limited in their time for
47 maximum acceleration due to restrictions on the quickly available energy. Consequently,
48 acceleration time becomes the critical factor determining the maximum speed of animals. In the
49 following, we first derive the maximum-speed model (in equations that are illustrated in the
50 conceptual Fig. 1) and, subsequently, test the model predictions employing a global data base
51 and eventually illustrate its applications to advance a more general understanding of animal
52 movement.

53 Consistent with prior models, we start with a power-law scaling of theoretical maximum speed

54 $v_{\max(\text{theor})}$ of animals with body mass M :

55
$$v_{\max(\text{theor})} = aM^b \quad (1)$$

56
57 During acceleration, the speed of an animal over time t saturates (Fig 1a, solid lines) approaching

58 $v_{\max(\text{theor})}$ (Fig 1a, dotted lines):

59
$$v(t) = v_{\max(\text{theor})} (1 - e^{-kt}) \quad (2)$$

60

61 The acceleration constant k describes how fast an animal reaches $v_{\max(\text{theor})}$. Based on the
62 Newtonian principle $F=M *k$, acceleration k should scale relative to the ratio between maximum
63 force, F , and body mass, M : $k \sim F/M$. Knowing that maximum muscle force is roughly proportional
64 to body mass as: $F \sim M^d$, this yields a general power law scaling of k with body mass M :

65
$$k = c M^{d-1} \quad (3)$$

66

67 with constants c and d . As the allometric exponent d of the muscle force falls within the range 0.75
68 to 0.94¹⁶⁻¹⁸ the overall exponent $(d-1)$ should be negative, implying that larger animals need more
69 time to accelerate to the same speed than smaller ones (conceptual Fig 1a, color code exemplifies
70 four animals of different size). Note that this general scaling relationship also allows for the special
71 cases of a constant acceleration across species or a linear relationship with body mass.

72 While prolonged high speeds are related to the maximum aerobic metabolism, maximum burst
73 speeds are linked to anaerobic capacity^{19,20}. For maximum aerobic speed, so-called slow twitch
74 fibers are needed, which are highly efficient at using oxygen for generating adenosine triphosphate
75 (ATP) to fuel muscle contractions. Thus, they produce energy more slowly but for a long period
76 of time before they fatigue and allow for continuous, extended muscle contractions. In contrast,
77 maximum anaerobic speed is fueled by a special type of so-called fast twitch fibers, which use
78 ATP from the ATP storage of the fiber until it is depleted. Thus, they produce energy more quickly
79 but also fatigue very fast and only allow for short bursts of speed. Consequently, the critical time
80 available for maximum acceleration τ is limited by the amount of fast twitch fibers and their energy
81 storage capacity. This storage capacity is correlated with the amount of muscle tissue mass, which
82 is directly linked to body mass. Thus, similar to the muscle tissue mass, τ should follow a power
83 law:

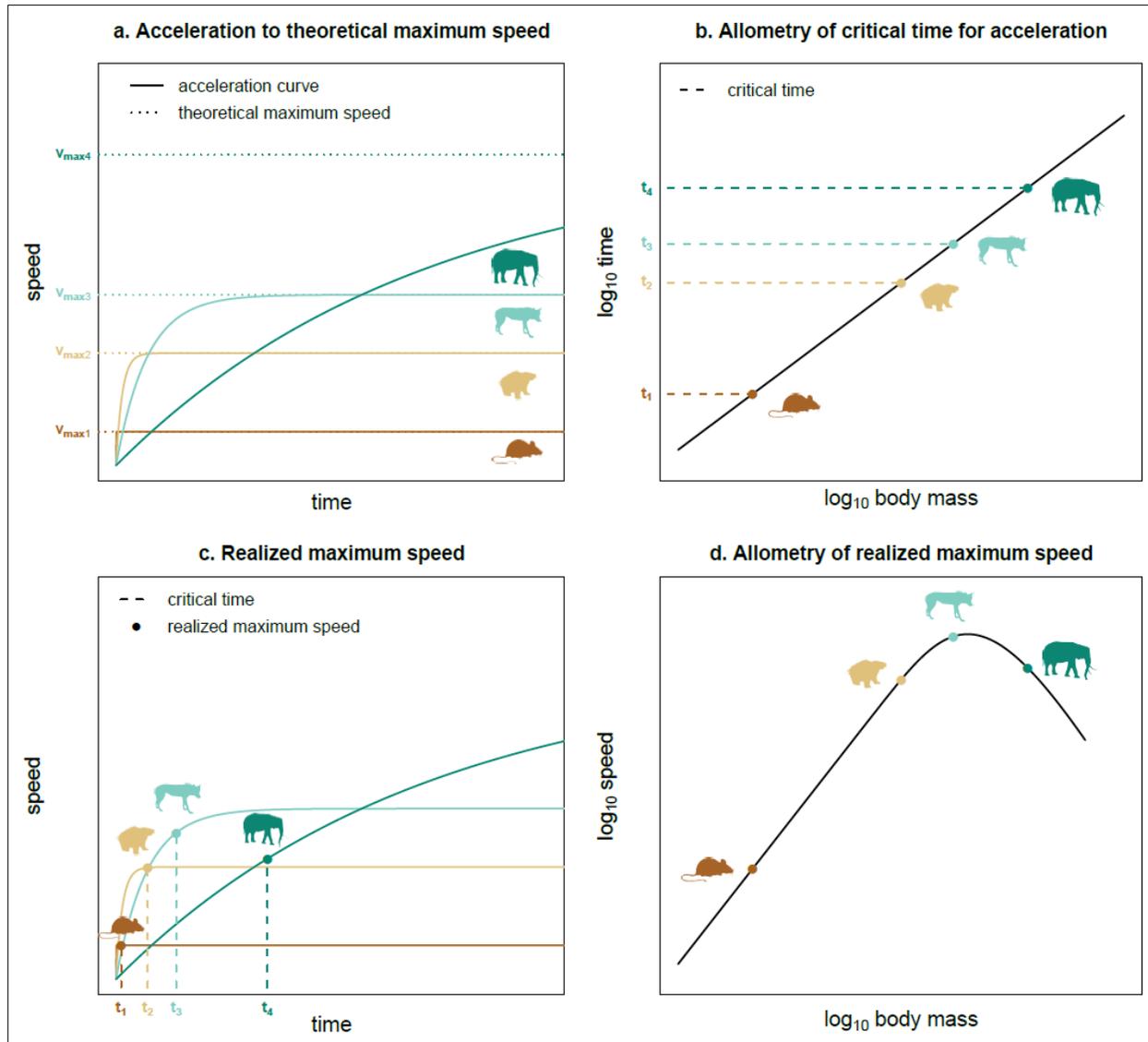
84
$$\tau = f M^g \quad (4),$$

85 where the allometric exponent g should fall in the range 0.76 to 1.27 documented for the allometric
86 scaling of muscle tissue mass^{21–24}. This power-law implies that larger animals should have more
87 time for acceleration (dashed red lines in conceptual Fig 1b and c). However, the power law
88 relationship of the critical time τ in our model allows for a negative or positive scaling of energy
89 availability with body mass as well as the lack of a relationship (constant energy availability across
90 body masses ($f=0$)). While we included power-law relationships of k and τ (equations 3 and 4) in
91 our model, these scaling assumptions are not strictly necessary. Instead, our only critical
92 assumptions are that acceleration over time follows a saturation curve (equation (1)) and that the
93 time available for acceleration is limited.

94 Within the critical time τ , after which energy available for acceleration is depleted, the animal
95 reaches its realized maximum speed v_{max} (points in Fig 1c), which may be lower than the theoretical
96 maximum speed (Fig 1a, dotted lines). Combining equations (1) – (4) with $t = \tau$ yields $v_{max} =$
97 $a M^b \left(1 - e^{-cfM^{d+g}}\right)$ which simplifies to

98
99
$$v_{max} = a M^b \left(1 - e^{-hM^i}\right) \quad (5)$$

100
101 where $1 - e^{-hM^i}$ is the limiting factor that determines the realized maximum speed depending on
102 the critical time and the body mass. This equation predicts a hump-shaped relationship between
103 realized maximum speed and body mass (conceptual Fig 1d). Based on the allometric power-
104 law exponents of muscle forces ($0.75 \leq d \leq 0.94$) and muscle mass ($0.76 \leq g \leq 1.27$), we expect that
105 the exponent i ($i=d-1+g$) should fall in the range between 0.51 and 1.21.



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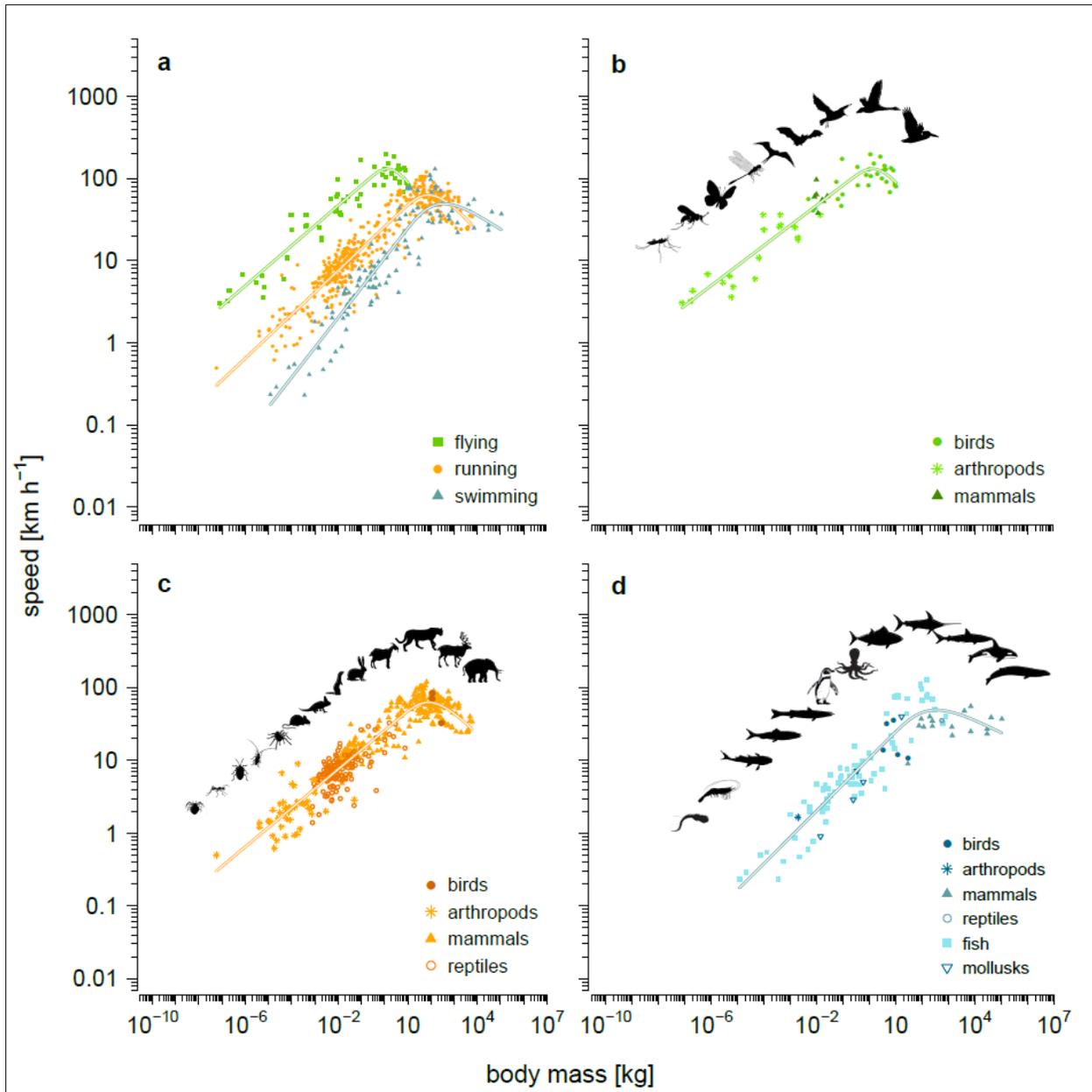
107 **Figure 1 | Concept of time- and mass-dependent realized maximum speed of animals.** Acceleration of animals
 108 follows a saturation curve (solid lines) approaching the theoretical maximum speed (dotted lines) depending on body
 109 mass (blue color code) (a). The time available for acceleration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

112 The limiting term $1 - e^{-hM^i}$ represents the fraction of the theoretical maximum speed that is
 113 realized and is defined on the interval $]0;1[$. For low body masses, this term is close to 1 and the
 114 realized maximum speed approximates the theoretical maximum speed (black and green dots in

115 Fig. 1c). With increasing body masses, this term decreases and reduces the realized maximum
116 speed (blue and yellow dots in Fig 1c). Put simply, small to intermediately sized animals accelerate
117 quickly and have enough time to reach their theoretical maximum speed whereas large animals are
118 limited in acceleration time and run out of readily mobilizable energy before being able to reach
119 their theoretically possible maximum speed. Therefore, they have a lower realized maximum speed
120 than predicted by a power-law scaling relationship.

121
122 To test the model predictions (Fig. 1d), we compiled literature data on maximum speeds of
123 running, flying and swimming animals including not only mammals, fish and bird species but also
124 reptiles, mollusks and arthropods. Body masses of these species range from 5.7×10^{-8} to 108,000
125 kg. Statistical comparison amongst multiple models (see Methods) shows that the time-dependent
126 maximum speed model is the most adequate (see Supplementary Table 3). Our model (Fig. 2,
127 parameter values in Supplementary Table 4) shows that the initial power-law increase of speed
128 with body mass is similar for running and flying animals ($b = 0.24$ and 0.27 , respectively).
129 However, flying animals are nearly six times faster than running ones ($a = 144$ and 26 ,
130 respectively). For swimming animals, the power-law increase in speed is steeper than expected (b
131 $= 0.36$, Fig 2a). This is due to the fact that in contrast to air (in which both flying and running
132 animals move), water is 800 times denser and 60 times more viscous²⁵. Small aquatic animals are
133 slower than running animals of the same body size while larger species approach a similar speed
134 as their running equivalents. This implies that in water, size brings a greater benefit in gaining
135 speed. The second exponent is higher for flying animals ($i = 0.72$) than for running ($i = 0.6$) and
136 swimming ones ($i = 0.56$), which fits into the expected range ($0.51 \leq i \leq 1.21$). Future research will
137 need to disentangle the relative importance of anaerobic and musculoskeletal constraints on

138 movement speed by measuring muscle force, muscle mass, body mass and maximum acceleration
139 for the same species to narrow down this large range of possible exponents. Furthermore, this may
140 allow to address the systematic differences in the exponent i between the locomotion modes as
141 well as potential morphological side effects (e.g. quadrupedal vs. bipedal running or soaring vs.
142 flapping flight).

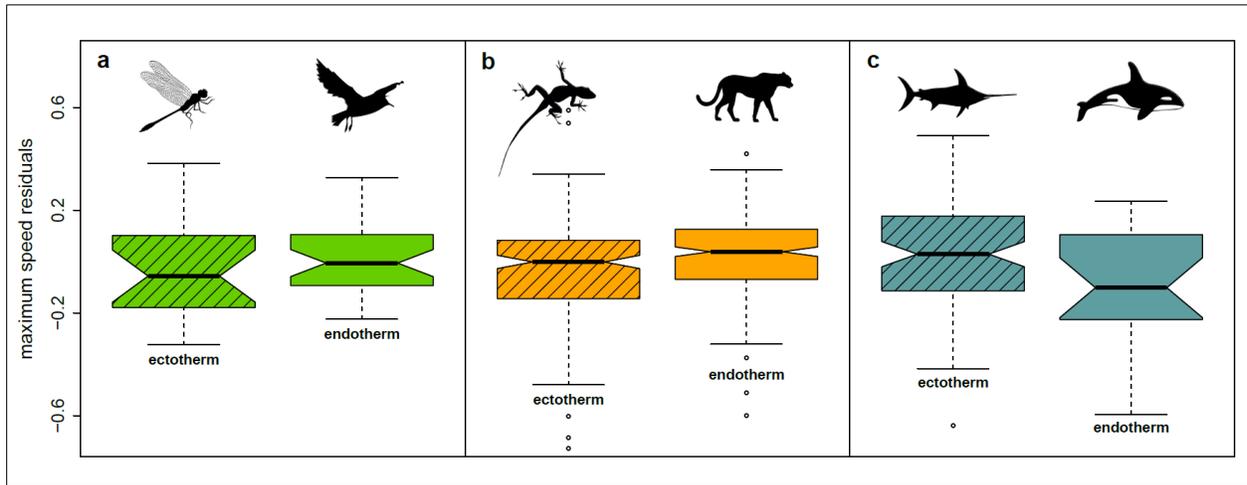


143
144 **Figure 2 | Empirical data and time-dependent model fit on the allometric scaling of maximum speed.** (a) Scaling
145 for the different locomotion modes (flying, running, swimming) in comparison. Taxonomic differences are illustrated
146 separately for (b) flying ($n = 55$), (c) running ($n = 453$) and (d) swimming ($n = 109$) animals. Overall model fit: $R^2 =$
147 0.893. The residual variation does not exhibit a signature of taxonomy (only a weak effect of thermoregulation, see
148 Methods).

149 While the model provides strikingly strong fits with observations ($R^2 = 0.893$), obvious
150 unexplained variation remains. This might partially be explained by the fact that our data probably

151 include not only maximum *anaerobic* speeds but also some slightly slower maximum *aerobic*
152 speeds. Moreover, we assessed the robustness of our model by exploring this residual variation
153 with respect to taxonomy (arthropods, birds, fish, mammals, mollusks, and reptiles), primary diet
154 (carnivore, herbivore, omnivore), thermoregulation (ectotherm, endotherm) and locomotion mode
155 (flying, running, swimming). As taxonomy and thermoregulation are highly correlated, we made
156 a first model without taxonomy and a second model without thermoregulation and compared them
157 by their BIC values (see Methods for details). According to this, the model including
158 thermoregulation instead of taxonomy is the most adequate ($\Delta\text{BIC} = 27.37$). In this model, the
159 differences between the diet types were not significant. In contrast, combinations of locomotion
160 mode with thermoregulation exhibited significant differences (Fig. 3). In flying and running
161 animals, endotherms generally tend to be faster than ectotherms (Fig. 3a and b). Metabolic
162 constraints may enable endotherms to have higher activity levels compared to ectotherms at the
163 low to intermediate temperatures most commonly encountered in nature²⁹. This pattern is reversed
164 in aquatic systems where endotherms (mammals and penguins) are significantly slower than
165 ectotherms (mainly fish, Fig. 3c). We assume that this is due to the transition from a terrestrial to
166 an aquatic lifestyle aquatic endotherms underwent. Semi-aquatic endotherms are adapted to
167 movement in two different media, which reduces swimming efficiency in comparison to wholly
168 marine mammals: they have 2.4×10^5 times higher costs of transport³⁰. But also in marine
169 mammals, costs of transport are considerably higher than in fish of similar size because they have
170 higher energy expenditures for maintaining their body temperature³⁰. Thus, the effect of
171 thermoregulation on the allometric scaling of maximum speed depends on the locomotion mode
172 and the medium. Overall, this significant effect of thermoregulation explained only ~ 4% of the

173 residual variation suggesting that the vast majority of the variation in speed across locomotion
174 modes, ecosystem types and taxonomic groups is well explained by our maximum speed model.



175
176 **Figure 3 | Effect of thermoregulation on the maximum speed of animals (residuals of the relationship in Fig. 2).**
177 In flying (a) and running (b) animals, endotherms are generally faster than ectotherms. In swimming animals (c) this
178 effect is reversed with ectotherms being generally faster than endotherms. Box plots show medians (horizontal line),
179 an approximation of 95% confidence intervals suitable for comparing two medians (notches), 25th and 75th percentiles
180 (boxes), the most extreme values within 1.5 times the length of the box away from the box (whiskers), and outliers
181 (dots).

182 Our findings help solve one of the most challenging questions in movement ecology over the last
183 decades: why are the largest animals not the fastest? Many studies tried to answer this based on
184 morphology, locomotion energetics and biomechanics¹⁰⁻¹⁴. However, the body-size related hump-
185 shaped pattern observed in empirical data on animal movement speed remained unresolved. To
186 account for this, some studies used polynomials but still lacked a mechanistic understanding²²⁻²⁴.
187 Others suggested a threshold beyond which animals run slower than predicted by a power-law
188 relationship due to biomechanical constraints¹³. Therefore, they propose different speed scaling
189 trends depending on the body-mass range^{11,12}. Instead of applying different laws to small and large
190 animals, we provide the first universal mechanistic model explaining the hump-shaped relationship

191 between maximum speed and body mass. Our speed predictions are thereby only derived from two
192 major species traits: body mass and locomotion mode, which explain almost 90% ($R^2 = 0.893$) of
193 the variation in maximum speed. This general approach allows a species-level prediction of speed
194 which is crucial for understanding movement patterns, species interactions and animal space use.

195 However, our model not only allows prediction of the speed of extant but also that of extinct
196 species. For example, paleontologists have long debated potential running speeds of large birds³¹
197 and dinosaurs^{32,33} roaming past ecosystems. The benchmark of speed predictions is set by detailed
198 morphological models^{32,33}. Interestingly, our maximum speed model yields similar predictions by
199 only accounting for body mass and locomotion mode (Table 1). For instance, in contrast to a
200 power-law model, the morphological and the time-dependent model predict lower speeds of
201 *Tyrannosaurus* compared to the much smaller *Velociraptor*. This is consistent with theories
202 claiming that *Tyrannosaurus* was very likely a slow runner³⁴. A simple power-law model only
203 yields reasonable results for lower body masses (e.g. flightless birds) while predictions for large
204 species such as giant quadrupedal dinosaurs are unrealistically high. In contrast, our time-
205 dependent model makes adequate predictions for small as well as large species (almost 80% of the
206 morphological speed predictions are within the confidence intervals of our model predictions,
207 Table 1).

208

209 **Table 1 | Maximum speed predictions** of extant and extinct flightless birds and bipedal and quadrupedal dinosaurs.
 210 Model predictions of a simple power law, morphological models and our time-dependent maximum speed model are
 211 compared (references in Supplementary Table 5). 95% confidence intervals (CI) are given for the power law and time-
 212 dependent model.

		taxa	mass [kg]	speed [km h ⁻¹]		
				power law (95% CI)	morphological models	time-dependent model (95% CI)
flightless birds	extant	 <i>Dromaius</i>	27.2	40.92 (38.58 - 43.40)	47.88	57.62 (47.65 - 60.91)
		 <i>Struthio</i>	65.3	49.33 (46.27 - 52.59)	55.44	62.75 (46.71 - 66.03)
	extinct	 <i>Patagornis</i>	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>	1400	94.87 (87.09 - 103.34)	33.84	40.78 (28.93 - 44.83)
		<i>Tyrannosaurus</i>	6000	129.41 (117.47 - 142.57)	28.8	27.05 (17.84 - 31.52)
quadrupedal dinosaurs		<i>Triceratops</i>	8478	139.32 (126.11 - 153.91)	26.4	24.36 (15.70 - 28.83)
		<i>Apatosaurus</i>	27869	179.59 (161.01 - 200.31)	12.3	16.75 (9.77 - 21.09)
		<i>Brachiosaurus</i>	78258	223.85 (199.00 - 251.80)	17.6	11.99 (6.39 - 16.04)

213
214

215 Our model also allows drawing inferences about evolutionary and ecological processes by
 216 analyzing the deviations of empirically measured speeds from the model predictions. Higher
 217 maximum speeds than predicted indicate evolutionary pressure on optimizing speed capacities that
 218 could for instance arise from co-evolution of pursuit predators and their prey. In ecological
 219 research, our maximum-speed model provides a mechanistic understanding of the upper limit to
 220 animal movement patterns during migration, dispersal or bridging habitat patches. The travelling
 221 speed characterizing these movements is the fraction of maximum speed that can be maintained
 222 over longer periods of time. The integration of our model as a species-specific scale (“what is

223 physiologically possible”) with research on how this fraction is modified by species traits and
224 environmental parameter such as landscape structure, resource availability and temperature (“what
225 is ecologically realized in nature”) can help provide a mechanistic understanding unifying
226 physiological and ecological constraints on animal movement. In addition to generalizing our
227 understanding across species traits and current landscape characteristics, this integrated approach
228 will facilitate the prediction of how species-specific movement and subsequently home ranges and
229 meta-communities may respond to the ongoing landscape fragmentation and environmental
230 change. Our approach may act as a simple and powerful tool for predicting the natural boundaries
231 of animal movement and help gain a more unified understanding of the currently assessed
232 movement data across taxa and ecosystems^{1,2}.

233

234 **Methods**

235 **Data.** We searched for published literature providing data on the maximum speeds of running,
236 flying and swimming animals by employing the search terms “maximum speed”, “escape speed”
237 and “sprint speed”. From this list, we excluded publications on (1) vertical speeds (mainly
238 published for birds) to avoid side-effects of gravitational acceleration that are not included in our
239 model or (2) the maxima of normal speeds (including also dispersal and migration). This resulted
240 in a data set containing 617 data points for 470 species (see Supplementary Table 1 for an
241 overview). Our data include laboratory and field studies as well as meta-studies (which are mainly
242 field studies but may also include a minor amount of laboratory studies). For some data points, the
243 study type could not be ascertained and they were marked as “unclear”. For an overview of the
244 study type of our data see Supplementary Table 2.

245

246 **Data availability:** The full data set is available on the iDiv data portal.

247

248 **Model fitting.** We fitted several models to these data: (1) the time-dependent maximum speed
249 model (equation (5)), (2) three polynomial models (a. simple polynomial model without cofactor,
250 b. polynomial model with taxon as cofactor but without interaction term and c. polynomial model
251 with taxon as cofactor with interaction term) and (3) three power law models (a. simple power law
252 without cofactor, b. power law with taxon as cofactor but without interaction term and c. power
253 law with taxon as cofactor with interaction term). For swimming animals, we excluded reptiles
254 and arthropods from the statistical analyses as they only contained one data point each (see
255 Supplementary Table 1). The polynomial and power law models were fitted by the `lm` function
256 and the time-dependent model by the `nls` function in R 3.2.3³⁵. The quality of the fits was compared
257 according to the Bayesian information criterion (BIC) that combines the maximized value of the

258 likelihood function with a penalty term for the number of parameters in the model. The model with
259 the lowest BIC is preferred, which demonstrates that the time-dependent maximum speed model
260 developed in the main text was most adequate in all cases (see Supplementary Table 3). For flying
261 animals, the simple polynomial model performed second best, whereas for running animals the
262 polynomial model with taxon as cofactor with interaction term and for swimming animals the
263 power-law model with taxon as cofactor with interaction term were second best (see
264 Supplementary Table 3). Overall, the lower BIC values indicate that the time dependent maximum
265 speed model provides a fit to the data that is substantially superior over power-law relationships,
266 models with taxonomy as cofactor or (non-mechanistic but also hump-shaped) polynomials. The
267 fitted parameter values of the time-dependent maximum speed model for flying, running and
268 swimming animals are given in Supplementary Table 4.

269

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

276

277 Model 1: residuals \sim (thermoregulation + diet type) * locomotion mode

278 Model 2: residuals \sim (taxonomy + diet type) * locomotion mode

279

280 We compared both models via BIC and carried out a further mixed effects model analysis on the
281 superior model. This model included the study type as a random factor influencing the intercept,
282 which ensures that differences among study types do not drive our statistical results. We
283 acknowledge that the direct inclusion of multiple covariates in the model-fitting process would be
284 preferable over residual analysis to avoid biased parameter estimates³⁶. However, this was
285 impeded by the complexity of fitting the non-linear model with four free parameters (equation (5)),
286 and our main goal was less exact parameter estimation than documenting the main variables
287 affecting the unexplained variation.

288

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366 **Author Contributions**

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

370 **Competing financial interests:** The authors declare no competing financial interests.