

1 **Title: Universal metabolic constraints shape the evolutionary ecology of diving**
2 **in animals**

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Abstract:

21 Diving as a lifestyle has evolved on multiple occasions when air-breathing terrestrial animals
22 invaded the aquatic realm, and diving performance shapes the ecology and behaviour of all air-
23 breathing aquatic taxa, from small insects to great whales. Using the largest dataset yet
24 assembled, we show that maximum dive duration increases predictably with body mass in both
25 ectotherms and endotherms. Compared to endotherms, ectotherms can remain submerged for
26 longer, but the mass scaling relationship for dive duration is much steeper in endotherms than in
27 ectotherms. These differences in diving allometry can be fully explained by inherent differences
28 between the two groups in their metabolic rate and how metabolism scales with body mass and
29 temperature. We therefore suggest that similar constraints on oxygen storage and usage have
30 shaped the evolutionary ecology of diving in all air-breathing animals, irrespective of their
31 evolutionary history and metabolic mode. The steeper scaling relationship between body mass
32 and dive duration in endotherms not only helps explain why the largest extant vertebrate divers
33 are endothermic rather than ectothermic, but also fits well with the emerging consensus that large
34 extinct tetrapod divers (e.g. plesiosaurs, ichthyosaurs and mosasaurs) were endothermic.

35

One Sentence Summary:

37 Constraints on oxygen storage and usage have shaped the ecology of all air-breathing divers,
38 from insects to whales.

39

Keywords:

41 allometry, ectothermy, endothermy, evolutionary physiology, palaeophysiology, scaling.

42

43

44 **Introduction**

45 Diving behaviour has evolved independently many times in air-breathing animals as diverse as
46 insects, amphibians, turtles, crocodiles, snakes, birds and mammals¹⁻⁶, as well as a number of
47 extinct reptile lineages⁷. The behaviour and ecology of these air-breathers depend on their ability
48 to remain submerged^{8,9}. All diving animals face the same basic challenges, and natural selection
49 generally should act to maximise dive duration within the constraints of an organism's
50 morphology and physiology. Body mass has an overriding influence on maximum dive
51 duration^{10,11} and, according to the *Oxygen Store/Usage Hypothesis*^{1,10,12}, larger-bodied species
52 should be better at 'holding their breath', because oxygen stores scale approximately
53 isometrically (m^1) with body mass, whereas oxygen requirements (metabolic rates) scale with
54 negative allometry ($m^{<1}$). Owing to their lower mass-specific metabolic rates, large divers can
55 store more oxygen relative to the rate at which they consume it. Support for this hypothesis is
56 particularly strong for endotherms^{10,13}, although one recent study suggests it may also apply to
57 ectotherms, albeit based on data limited to vertebrates¹². A high metabolic rate is the main source
58 of heat in endotherms, and their elevated metabolic rates whilst at rest enable them to maintain a
59 relatively-high and more-or-less constant internal temperature (homeothermy)¹⁴⁻¹⁶. By this
60 definition, endothermy in modern faunas is restricted to birds and mammals, although we
61 acknowledge that some large ectotherms can attain and maintain relatively constant body
62 temperatures (i.e. "gigantothermy" and "inertial homeothermy", such as the leatherback turtle
63 *Dermochelys coriacea*).

64 Here we examine how metabolic constraints govern limits to diving performance across
65 air-breathing taxa as different as small insects and large cetaceans within a phylogenetic
66 framework and consider the implications for our understanding of diving in both extant and

67 extinct animals. To date, formal tests of the *Oxygen Store/Usage Hypothesis* in ectotherms have
68 been hampered by the lack of empirical data for small-bodied taxa¹¹. However, recent works^{6,17}
69 have generated data on the diving behaviour of 26 species of insects (see Fig. 1), greatly
70 broadening the phylogenetic representation and, most importantly, extending the body mass
71 range of ectotherms available for analysis. In fact, these new data enable the comparative study
72 of ectothermic animals ranging over approximately eight orders of magnitude in body mass,
73 from small diving beetles (*Deronectes bicostatus* approx. 5.5 mg¹⁷) to large sea turtles
74 (*Dermochelys coriacea* > 300 Kg¹⁸). Drawing on the largest dataset compiled to date on dive
75 duration and body mass in both ectotherm and endotherm divers, we test whether the *Oxygen*
76 *Store/Usage Hypothesis* applies to all diving animals, irrespective of their evolutionary origin
77 and metabolic mode. Specifically, we compiled and analysed 1,792 records for 286 species,
78 including 62 ectotherms and 224 endotherms. This represents an increase of 78%, 121% and
79 10% for total number of records, ectotherm species, and endotherm species, respectively,
80 compared to the last update¹² (Fig. S1A). To do so, we quantify the body mass dependence of
81 maximum dive duration in both ectotherm and endotherm divers, and compare empirical scaling
82 relationships of dive duration with the known mass dependency of metabolic rate (oxygen
83 consumption) in the two groups (see Methods for more details on selection of appropriate scaling
84 coefficients). Metabolic rate increases with body mass, but less strongly in endotherms than
85 ectotherms, as reflected in scaling exponents for resting metabolic rate being lower for
86 endotherms than ectotherms, both on empirical and theoretical grounds: see ref^{19,20,21}, Methods
87 and supplementary analyses. Consequently, if the *Oxygen Store/Usage Hypothesis* holds true,
88 scaling exponents for maximum dive duration should be smaller in ectotherms than endotherms,
89 and this difference should be attributable to differences in metabolic scaling between the two

90 groups²². Metabolic rate also increases with temperature and therefore we also included body
91 temperature (where available) or water temperature in our analyses. Our working assumption is
92 that diving in both ectotherms and endotherms is governed by the same general principles,
93 meaning that differences in maximum dive duration should be mirrored by differences in
94 metabolic rate, related to differences in body mass and temperature. As a result, the lower
95 oxygen requirements of ectotherms should enable them to remain submerged for longer than
96 similarly sized endotherms¹¹, whereas the steeper metabolic scaling in ectotherms¹⁹ should
97 translate to smaller gains in diving performance with increasing body mass.

98

99 **Results**

100 Maximum dive duration varied from less than a minute in several birds to greater than 1 h in
101 several turtle species and some cetaceans. Much of the variation in maximum dive duration can
102 be accounted for by metabolic mode (endothermy vs. ectothermy), body mass, and temperature
103 (Table 1). The model best fitting the data employed phylogenetic generalized least squares
104 (PGLS) based on a time-calibrated phylogenetic tree that was rescaled by Grafen's rho ($\rho =$
105 0.273). This model significantly outperformed a PGLS using a star phylogeny ($\lambda = 0$; $\Delta\text{AIC} =$
106 91.1) and a PGLS with a lambda close to 1 ($\lambda = 0.95$; $\Delta\text{AIC} = 13.8$). Dive duration increased
107 with body mass in both ectotherms and endotherms (Fig. 2A, $P < 0.021$), but scaling exponents
108 differed significantly, with dive duration increasing more steeply with body mass in endotherms
109 (body mass x metabolic mode interaction, $P = 0.022$). As an example, maximum dive duration
110 increased almost 11-fold with a 1,000-fold increase in body mass in endotherms, but only around
111 3-fold in ectotherms. In order to test whether these differences in diving allometry can be
112 explained from known differences in metabolic scaling between ectotherms and endotherms, we

113 regressed dive duration against an index of oxygen storage capacity, instead of body mass. This
114 index accounts for mass-related differences in oxygen usage and storage (see Methods). When
115 substituting body mass for this index, we no longer found that dive duration scaled differently
116 between ectotherms and endotherms (i.e. the interaction between the Oxygen index and
117 Metabolic mode was non-significant; $P = 0.91$), the model without the interaction performing
118 better ($\Delta AIC = 2.1$; Table 1; Fig. 2B). Very similar results were obtained here when using a
119 time-calibrated phylogeny where lambda was estimated ($\lambda = 0.95$) or a star phylogeny ($\lambda = 0$)
120 (see Table 1).

121 We also found differences in intercepts (elevations) between ectotherms and endotherms;
122 dive duration being greater in ectotherms than endotherms of comparable body mass (Fig. 2A,
123 Table 1). As differences in mass scaling complicate comparisons of intercepts, we based our
124 exploration on the best fitting model employing the index of oxygen storage capacity (Fig. 2B;
125 model C in Table 1), meaning that such differences in scaling were accounted for. Based on that
126 model, dive duration in ectotherms was about an order of magnitude longer than in endotherms
127 with a comparable oxygen storage capacity. Finally, in all models, we found that dive duration
128 was significantly affected by differences in temperature across species (Table 1, Fig. 2C). In all
129 cases the effect of the temperature correction factor was negative, meaning that the greater rate
130 of oxygen consumption associated with elevated temperatures (see Fig. S3) resulted in a shorter
131 dive duration. Since temperature exponentially increases metabolic rate, the effect of temperature
132 is curvilinear (Fig. 2C) and the fitted value for the temperature correction factor in the model ($-$
133 0.864 ± 0.282) was indeed close to the expected value of -1 , where any increase in oxygen
134 demand would reduce dive duration by the same factor.

135

136 **Discussion**

137 Our work provides an unprecedented analysis of the physiological and evolutionary ecology of
138 diving behaviour from a metabolic perspective with far-reaching implications. We reveal clear
139 differences in the mass scaling of maximum dive duration between ectotherms and endotherms
140 and show that these different scaling relationships can be reconciled from known differences in
141 the mass scaling of metabolic rates between ectotherms and endotherms as predicted from the
142 *Oxygen Store/Usage Hypothesis*^{1,10,22}. As with endotherms, the diving performance of
143 ectotherms has not evolved independently of body mass¹¹, and the same basic physiological
144 principles have apparently shaped the evolutionary ecology of diving in all animals, from small
145 diving beetles to great whales^{11,12,17,23}.

146 In the past, the relative paucity of data for ectotherm divers, has prevented rigorous
147 testing of the *Oxygen Store/Usage Hypothesis* across all diving animals. Our analyses
148 demonstrate that previous uncertainty regarding the scaling of dive duration with body mass in
149 ectotherms was a result of the lack of information on small ectotherm divers, and not because
150 ectotherms are more phylogenetically diverse than endotherms, or because they display greater
151 metabolic variation¹¹. In fact, the vertical scatter around the allometric relationships is similar for
152 ectotherms and endotherms. Such scatter shows that there is variation in diving capacity between
153 species of similar size or phylogeny, highlighting that in particular lineages and species, body
154 mass and oxygen storage capacity may be uncoupled to some extent (Fig. 2A; see also^{11,13}). The
155 evolution of particular physiological adaptations may often explain such uncoupling. For
156 example, the elevated hematocrit level found in marine snakes (Hydrophiinae) facilitates
157 increased aerobic dive duration⁴. Many diving mammals have evolved myoglobins with elevated
158 net surface charge, which facilitates higher intramuscular concentrations²⁴. Conversely, lunge-

159 feeding in balaenopterid rorquals is energetically costly and the evolution of lunge-feeding
160 appears to have compromised their diving capacities²⁵. Given the allometry of diving we report
161 here, such adaptations appear to be modulations superimposed upon the universal constraints of
162 size-dependent oxygen storage and utilisation.

163 Greater gains in dive capacity with body mass are predicted under the *Oxygen*
164 *Store/Usage Hypothesis* for endotherms, since their mass-specific rates of oxygen consumption
165 decline more with increasing body mass compared to ectotherms¹, something which is supported
166 by empirical studies showing that scaling exponents for resting metabolic rate are lower for
167 endotherms than ectotherms^{19,20}. The mass-related differences between the dive duration of
168 ectotherms and endotherms reported here (Fig. 2A) are fully mirrored by mass-related
169 differences in their metabolic rates; not just in slopes, but also intercepts (Fig. 2B). Differences
170 in slopes disappeared when we accounted for differences in oxygen storage relative to usage,
171 using the index of oxygen storage capacity. The modelled slope for the oxygen index is close to
172 1, indicating a proportional relationship (Fig. 2B; Table 1), which makes sense as animals should
173 gain dive capacity in proportion to their capacity to store oxygen, once differences in oxygen
174 demand are accounted for. A sensitivity analysis, employing different scaling exponents for
175 ectotherm and endotherm metabolic rates (derived from a reanalysis of the largest database
176 available on these rates - see supplementary materials) yielded similar results (see Table S1). Our
177 demonstration of differences between ectotherms and endotherms in the mass scaling of dive
178 duration contrasts with previous analyses, limited to vertebrates¹², that did not find such
179 differences. The greater range of animal body sizes in our study, including larger (leatherback
180 turtles) and smaller (dytiscid beetles) ectotherms, likely enabled us to detect these differences in
181 scaling. The maximum dive duration of endotherms and ectotherms converged at large body

182 sizes, whereas there was no difference in scaling exponents when comparing endotherms and
183 ectotherms on the basis of index of oxygen storage capacity (Table 1, model B). Considering
184 differences in intercepts, for a given oxygen index, ectothermic divers such as reptiles can
185 remain submerged for much longer than their endothermic counterparts¹¹. Such greater dive
186 duration in ectotherms is partly related to their lower body temperature and partly to their
187 metabolic mode; effects of the latter accounting for a 10-fold difference in dive time (Model C,
188 Table 1). This is in line with the observation that absolute metabolic rates are generally around
189 an order of magnitude lower in ectotherms compared to endotherms, when expressed at a
190 common temperature²⁶⁻²⁸ - see also supplementary analysis. Although the largest ectotherms
191 approach the same dive duration as similarly sized endotherms, they will have smaller lower
192 oxygen consumption rates and concomitantly smaller oxygen stores. Oxygen stores scale
193 approximately isometrically with body mass, but the differences in metabolic scaling results in a
194 shallower mass scaling of dive duration in ectotherms, meaning that the benefits of ectothermy
195 for diving duration are reduced at large body sizes.

196 Since temperature increases metabolic rate, higher temperatures result in lower dive
197 durations and as temperature has an exponential effect, stronger reductions are both expected and
198 observed towards higher body temperatures in endotherms (Fig. 2C). This non-linearity was
199 encapsulated by our temperature correction factor, which expresses the effect temperature has on
200 oxygen demand, relative to a reference temperature (see Fig. S3). As such, it represents a
201 multiplication factor for metabolism. According to the *Oxygen Store/Usage Hypothesis*, any
202 temperature-driven increase in oxygen demand should translate to an equivalent reduction in
203 dive duration. As dive duration on a \log_{10} scale also represents a multiplication factor, the
204 hypothesis will be supported if the model has a fitted value of -1, which closely matches the

205 value observed in our analyses (Table 1). In summary, the values estimated for intercepts and
206 slopes indicate that dive duration increases proportionally with oxygen storage capacity (as
207 shown by the index of oxygen storage capacity) and that it decreases proportionally with
208 temperature-driven increases in oxygen demand (as shown by the temperature correction factor).
209 A metabolic perspective on dive duration is therefore further supported by the fitted values for
210 both thermal dependence and scaling of metabolism.

211 Air contains 20-30x more oxygen than water, is less viscous and less dense and
212 consequently rates of oxygen diffusion are ~300,000 times faster in air than in water^{29,30}. Large
213 animals are therefore much better able to meet their metabolic demands by breathing air rather
214 than obtaining oxygen from water, which could partly explain why the largest aquatic animals to
215 have evolved are air-breathing divers rather than fishes³¹. Today, the largest diving animals are
216 all true endotherms (Cetacea). Although endothermy in itself is not a prerequisite to be a good
217 diver, it may have facilitated the evolution of large body size. Recent studies of bone and soft
218 tissue anatomy^{7, 32-34}, as well as the oxygen isotope composition of tooth phosphate^{35,36}, suggest
219 that ichthyosaurs, plesiosaurs and mososaurs, and perhaps some other extinct marine reptile
220 groups, were also truly endothermic. As well as allowing increased aerobic capacity^{14,37},
221 endothermy facilitates the colonisation of a wide range of marine habitats, including relatively
222 cold seas, known to have been occupied by such marine reptiles^{35,38}. Although the fossil record
223 of these taxa is punctuated by extinction events which reduce morphological diversity (e.g. ref³⁹),
224 all three groups contain species that achieved very large body sizes, in some cases comparable to
225 some of the largest modern cetaceans⁴⁰, and show evidence of increases in body size with
226 time^{39,41,42}. Because the scaling exponents for metabolic rate are lower for endotherms when
227 compared to ectotherms, net gains in dive duration *per* unit mass increase are greater in

228 endothermic animals. Although many other factors clearly influence body size, this extra
229 advantage of being large may, at least in part, have facilitated the evolution of large body size in
230 both extinct and extant tetrapod divers.

231 At the macroevolutionary level, once differences in metabolic rate are accounted for, both
232 endothermic and ectothermic animals converge on the same allometric relationship when
233 considering how long they can hold their breath. This pattern suggests that the adaptive
234 significance of body size and metabolism for dive duration is largely independent of
235 evolutionary history. Viewed through the lens of the *Oxygen Store/Usage Hypothesis*, body mass
236 and temperature affect dive duration in a similar manner in taxa as evolutionarily distant as
237 insects, reptiles, birds and mammals. Consequently, the same general physical and physiological
238 principles have shaped the evolution of diving in all animal groups, both ancient and modern,
239 constituting a new fundamental principle for evolutionary physiology^{43,44}.

240

241 **Materials and Methods**

242 *Data collection and selection*

243 Data on diving performance and body mass of ectotherms and endotherms were collated
244 from the published literature. We have drawn on a previously published dataset, initially
245 constructed by Schreer and Kovacs³ and subsequently updated by Halsey *et al.*¹⁰, Brischoux *et*
246 *al.*¹¹ and Hayward *et al.*¹². We used the "penguiness book"⁴⁵ to locate most of the studies used.
247 We rechecked all records and added data from the primary literature to generate the most
248 comprehensive dataset on dive duration to date, comprising 1,792 records for 286 species of
249 which 62 were ectotherms and 224 endotherms (Fig. S1A).

250 We focused on maximum dive duration as a proxy for the evolutionary limit to dive
 251 capacity in a given species. Preliminary analyses showed that maximum dive duration co-varied
 252 closely with mean dive duration (Fig. S2A), even after accounting for differences in body mass
 253 and temperature (Fig. S2B). For species with multiple data entries for maximum dive duration,
 254 we selected the entry closest to the 95th percentile, in an attempt to account for variation in
 255 sample size across species⁴⁶. For species with many records, the absolute longest dive recorded
 256 may also sometimes represent an extreme event, such as an animal being disoriented. Taking the
 257 95th percentile will help to minimise the influence of such events. Temperature strongly affects
 258 metabolic rate in ectotherms²⁶, see also supplementary analysis, and hence also affects dive duration (e.g.
 259 ^{6,17,47,48}). Selection of the data entry closest to the 95th percentile for a given species was therefore
 260 based on dive duration expressed at a common mean temperature, by correcting dive duration
 261 with a (within-species) temperature correction factor:

262

$$263 \quad \text{Temperature correction factor} = e^{\frac{-Ea}{k} * (1/Temperature - 1/Mean\ temperature)}$$

264

265 where Ea is the activation energy in eV and k is the Boltzmann constant in eV·K⁻¹ and
 266 $Temperature$ is expressed in Kelvin. Here we used an Ea of 0.68 eV, which roughly equates to a
 267 Q_{10} of 2.4, as is typically found in intraspecific comparisons (see Supplementary Materials).
 268 Temperature values refer to body temperature where available (all endotherms and some
 269 ectotherms) and otherwise to water temperature (most ectotherms). The common mean
 270 temperature represented the mean across all species in the database (33°C); at this mean
 271 temperature the temperature correction factor = 1. By selecting the data entry of the individual
 272 whose dive duration was closest to the 95th percentile (see above), we assembled data on body

273 mass, temperature, and maximum dive duration for the 226 species for which we had data on
274 maximum dive duration and these data were used in further analyses (see Fig. S1B). We
275 excluded the very high submergence times (>30,000 min) reported for the Fitzroy River turtle,
276 *Rheodytes leukops*, since these represent brumation events rather than dives. During brumation
277 metabolic rates are greatly reduced and *R. leukops* survives by aquatic respiration across the
278 surface of the cloacal bursae⁴⁹.

279

280 *Data analyses*

281 We explored the effect of body mass on dive duration using linear versions of phylogenetic
282 generalized least squares (PGLS) models. These models were used to test whether the mass
283 scaling of diving performance differed between ectotherms and endotherms, both in terms of
284 intercept, which would indicate absolute differences in dive capacity, and slope, which would
285 indicate differences in the mass dependence of diving performance. Both body mass and dive
286 duration were log₁₀-transformed prior to analyses. In each model we tested for differences in the
287 scaling exponent between ectotherms and endotherms by including an interaction term of body
288 mass x metabolic mode (i.e. ectotherm or endotherm). As temperature is known to affect dive
289 duration (see above), some variation in dive duration across species is likely attributable to
290 differences in body temperature. Based on the *Oxygen Store/Usage Hypothesis*, such thermal
291 effects should be mediated through the effect temperature has on metabolic rate. To capture the
292 non-linear effect of temperature on metabolism, we calculated a temperature correction factor
293 using the equation above, rather than including temperature directly. Preliminary analyses
294 confirmed that models which employed this correction factor were better supported than those
295 using raw temperatures. Since we are making across-species comparisons here, we employed the

296 activation energy reported for interspecific comparisons (i.e. $Ea = 0.43\text{eV}$ ref⁵⁰; Fig. S3), which
297 roughly corresponds to a Q_{10} of 1.7. Although it is well established that thermal activation
298 energies differ when making comparisons across or within species, we also ran sensitivity
299 analyses to determine whether our conclusions were robust to different values for activation
300 energy. These analyses yielded similar results for both 25% lower and 25% higher activation
301 energies (see Table S2). As expected, fitted values for temperature differed slightly, but in all
302 cases, temperature significantly affected dive duration and in all cases we found a clear
303 difference in dive allometry between ectotherms and endotherms. Preliminary analyses also
304 explored whether ectotherms and endotherms differed in the thermal sensitivity of their dive
305 durations, by including an interaction between metabolic mode and the temperature correction
306 factor. However, such models were uninformative, as endotherms and ectotherms differed both
307 with respect to body mass and body temperature, making it impossible to disentangle the relative
308 importance of these parameters when both are allowed to vary. Birds, with their relatively low
309 dive durations, are both smaller and warmer compared to mammals. Similarly, endotherms are
310 both larger and warmer than ectotherms. Due to this covariation between body size and body
311 temperature across clades, we calculated the thermal effect on metabolism using the same value
312 across all species (see Fig S3), rather than fitting them separately in the models. Studies that
313 investigate the thermal sensitivity of metabolic rate in ectotherms suggest that although species
314 differ, a single value for activation energy can approximate the thermal sensitivity in large-scale
315 comparisons²³, including in the context of diving¹².

316 Under the *Oxygen Store/Usage Hypothesis*, an isometric increase in oxygen stores (M^1)
317 and a suballometric increase in metabolism (M^β , with $\beta < 1$) generate an increase in oxygen
318 storage capacity relative to metabolic demand with increasing body mass; a similar argument is

319 used to predict the positive scaling of fasting endurance with body mass⁵¹. In order to account for
320 such mass related differences in metabolism, and test whether these differences in diving
321 allometry can be explained from known differences in metabolic scaling between ectotherms and
322 endotherms, we regressed dive duration against an index of oxygen storage capacity, instead of
323 body mass. This index of oxygen storage capacity is defined as:

324

$$325 \quad \text{O}_2 \text{ index} = M^{1-\beta}$$

326

327 where β is the metabolic scaling exponent. Empirical evidence indicates that the metabolic
328 scaling exponent differs between endotherms and ectotherms^{19,20}, which Glazier²¹ explained with
329 his ‘metabolic-level boundaries hypothesis’. Consequently, this index was calculated based on
330 their respective scaling exponents. Although many different exponents have been reported in the
331 literature, we considered the most applicable to be values that were phylogenetically corrected
332 and included weighted means with random effects (i.e. 0.837 for ectotherms and 0.670 for
333 endotherms)¹⁹. Moreover, these values for the scaling exponents align very closely with those
334 based on field metabolic rates reported in the same paper. We also ran a sensitivity analysis to
335 explore how different values for the scaling exponents observed in endotherms and ectotherms
336 influenced our analysis. The scaling exponents used for this were based on a re-analysis of
337 metabolic rates compiled from the literature⁵² and yielded similar results: when correcting for
338 differences in metabolic scaling we never found different slopes for ectotherms and endotherms.
339 Also, the model fitted a value for the oxygen index that was close to 1 (Table S1).
340 The correlation structure of PGLS models reflects the potential similarity of species’ traits
341 resulting from shared evolutionary history and an assumed model of residual trait evolution (e.g.,

342 see ⁵³⁻⁵⁵). These models can incorporate a transformation parameter that, in essence, stretches the
343 internal nodes of the tree either towards the tips of the tree (implying more phylogenetic signal in
344 the residual trait values) or towards the root of the tree (implying less phylogenetic signal in the
345 residuals). Given that we compare animals as different as turtles and diving beetles, accounting
346 for the influence of phylogeny is not straightforward. Therefore, we have considered different
347 transformation parameters and compared their goodness of fit (see Supplementary Materials; Fig.
348 S4). One such transformation parameter is Pagel's lambda (λ)⁵⁶. A value for lambda close to zero
349 indicates low phylogenetic signal (phylogenetic independence between species' residuals, or a
350 star phylogeny), whilst a value closer to one suggests that species' traits evolved randomly
351 through evolutionary timescales via a process similar to Brownian motion. It is also possible to
352 scale branches differently, depending on the position relative to the root by using Grafen's⁵⁷ rho
353 (ρ). For values of ρ near 0, branches near the tips are expanded, whilst for values above 1,
354 branches near the root are compressed, and vice versa. We constructed a topological tree for all
355 species in our dataset, drawing on published phylogenies⁵⁸⁻⁶² (Fig. 1) and added branch length
356 estimates using TimeTree⁶³. We then considered transformation effects of either Pagel's lambda
357 (λ) or Grafen's rho (ρ) and compared the goodness of fits (Table 1). Both transformation effects
358 had a clear optimum (Fig S4), which significantly improved upon the non-phylogenetic analysis
359 (λ) and the untransformed time calibrated tree ($\lambda=1$) (Table 1). We also considered Ornstein–
360 Uhlenbeck (OU) models, in the ape and nlme packages. Whilst these fitted the data (alpha =
361 0.102) and gave parameter estimates similar to the best fitting model in Table 1, model support
362 was much lower (AIC = 182.48). This could result since it is unlikely that there is a single
363 attractor in our models: e.g. beetles and whales are unlikely to share a common optimal body
364 size. Whilst this could theoretically be solved by running OU models with multiple optima, this

365 would require good priors and may result in overfitting of the data. Consequently, we did not
366 pursue this approach further. Finally, we fitted an additional model that excluded the effects of
367 phylogeny: i.e. with $\lambda = 0$, which yields a star phylogeny and has one fewer parameter in the
368 model.

369 All analyses were performed in R, using the packages *ape*, *picante*, *caper*. Residual plots (Figs.
370 S5) were visually inspected for homoscedasticity, normality, and other assumptions. Effects of
371 model variables are illustrated by means of partial residual plots using the package *visreg*. Partial
372 residual plots illustrate the relationship between the independent variable and a given response
373 variable whilst accounting for the effects of other independent variables in the model. Such plots
374 are constructed by adding the residuals of the model to the fitted relationship of the independent
375 variable of interest and plotting these values (on the y-axis) against the independent variable of
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377

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396

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537

538 Supplementary Materials:

539 Supplementary analysis: differences in metabolic scaling exponent between ectotherms and
540 endotherms.

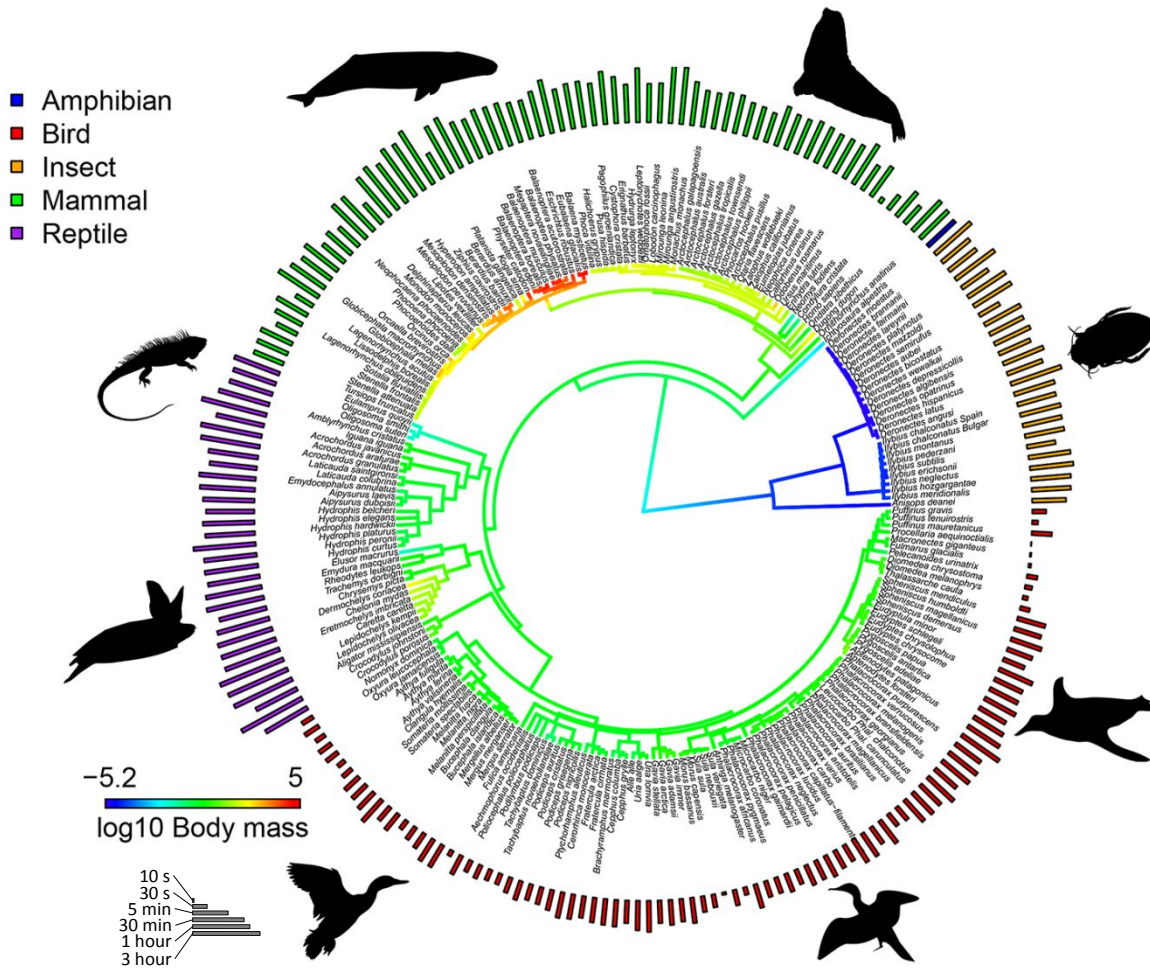
541 Sensitivity analyses: sensitivity to: 1) different scaling exponents; 2) different activation
542 energies; 3) different transformations of the phylogenetic tree.

543 Figures S1-S4

544 Tables S1, S2

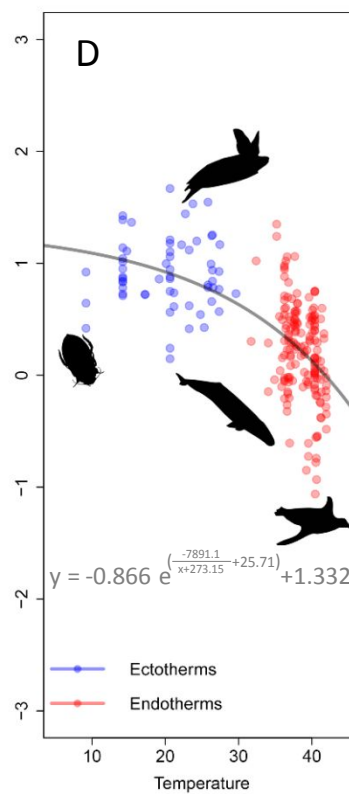
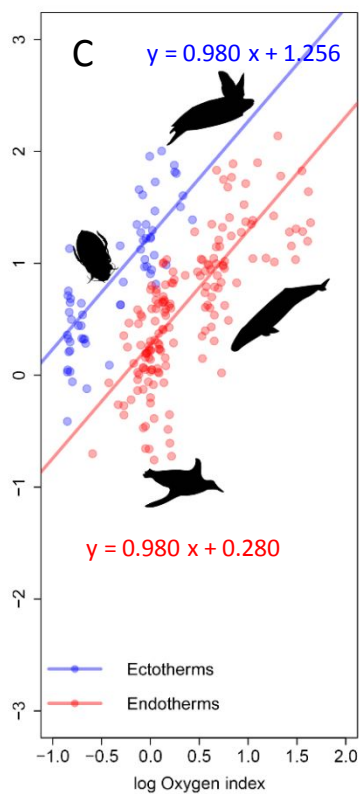
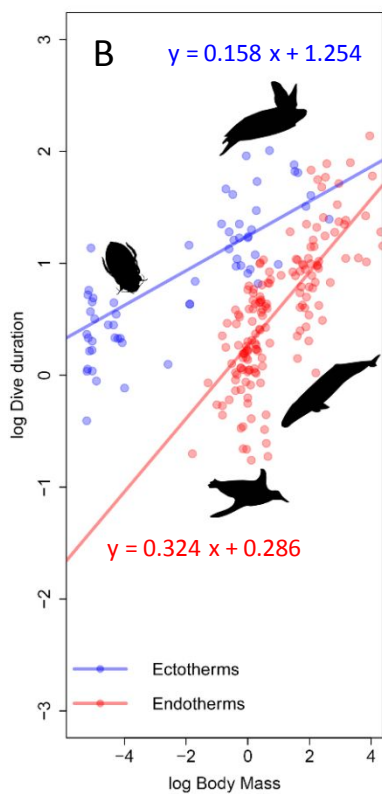
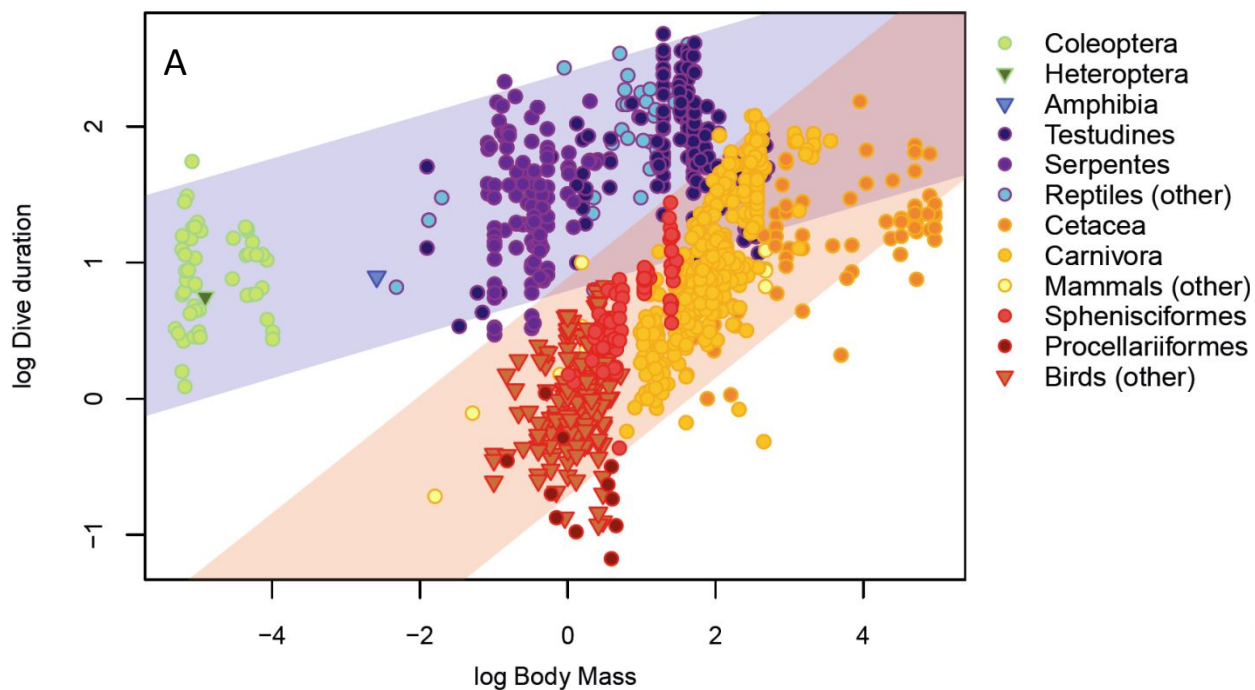
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 548 **Fig. 1.** Phylogenetic tree of all species (N=226) used in the analyses, displaying maximum dive
 549 duration (length of outer bars) and body mass (gradient in branch colours). Outer bars are colour
 550 coded to represent Reptiles (purple), Mammals (green), Insects (orange), Birds (red) and
 551 Amphibians (blue). For image credits see supplementary materials.

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553

554

555 **Fig. 2.** Plots with all the data on maximum dive duration, colour coded for different groups of
556 animals (A), with 95% prediction intervals shown separately for ectotherms (in blue) and
557 endotherms (in red). Partial residual plots show how maximum dive duration (min) changes with
558 body mass (kg) (B), the index of oxygen storage capacity (C), and temperature (D), whereby
559 species are colour coded according to being ectotherms (blue) or endotherms (red). Note the
560 \log_{10} transformation for Dive duration, Body mass and the Oxygen index. Linear regression
561 equations are given in each plot (full details on the parameters can be found in Table 1). Partial
562 residual plots illustrate the relationship between the response variable (here maximum dive
563 duration) and a given independent variable whilst accounting for the effects of other independent
564 variables in the model. Hence variation in dive duration owing to differences in temperature is
565 accounted for in plot B and C, isolating the effects of body mass and the oxygen index
566 respectively, whereas plot D isolates the effects of temperature by accounting for differences in
567 body mass. For image credits see supplementary materials.

568 **Table 1.** Summary of phylogenetic generalized least squares (PGLS) models to explain variation in maximum dive duration (log-
 569 transformed). Models employed either body mass (log-transformed) directly (model A), or an oxygen index based on body mass
 570 (models B and C; see Methods). In addition, models A and B included an interaction between metabolic mode and body mass or the
 571 oxygen index. All models also included the effect of temperature, expressed as the effect temperature has on oxygen demand (see Fig.
 572 S3), so that higher values indicate higher metabolic demand and hence reduced dive duration (see methods). Each model was analysed
 573 with a tree topology based on either a star phylogeny (thus defaulting to an OLS analysis), a tree with branch lengths estimated as
 574 divergence times, employing either no transformations, a transformation based on an optimal value for Pagel's lambda (λ) or Grafen's
 575 rho (ρ) (see Fig. S4). Parameter estimates are given with the standard error in brackets. AIC is the Akaike Information Criterion, with
 576 lower values indicating better fit of the model to the data. BIC is the Bayesian Information Criterion.

577
 578

A. Maximum dive duration ~ Body mass + Metabolic mode + Temperature + Body mass x Metabolic mode

tree topology	star ($\lambda=0$)		time-calibrated branch lengths (no branchlength transformations)		Optimal Lambda ($\lambda=0.95$)		Optimal Rho ($\rho = 0.273$)	
	Estimate (\pm SE)	P-value	Estimate (\pm SE)	P-value	Estimate (\pm SE)	P-value	Estimate (\pm SE)	P-value
Intercept: ectothermy	2.405 (\pm 0.160)	<0.0001	2.859 (\pm 1.968)	0.1477	2.009 (\pm 0.688)	0.0038	2.117 (\pm 0.257)	<0.0001
Body mass: ectothermy	0.197 (\pm 0.021)	<0.0001	0.3106 (\pm 0.198)	0.1183	0.124 (\pm 0.102)	0.2283	0.158 (\pm 0.054)	0.0039
Metabolic mode: endothermy	-0.864 (\pm 0.227)	0.0002	-0.179 (\pm 1.312)	0.8918	-0.823 (\pm 0.483)	0.0895	-0.968 (\pm 0.321)	0.0029
Temperature	-1.068 (\pm 0.261)	0.0001	-1.938 (\pm 0.441)	<0.0001	-0.993 (\pm 0.328)	0.0027	-0.863 (\pm 0.289)	0.0031
Body mass x Metabolic mode: endothermy	0.105 (\pm 0.041)	0.0108	0.016 (\pm 0.214)	0.9397	0.207 (\pm 0.112)	0.0663	0.167 (\pm 0.072)	0.0218
Log likelihood	-111.9802		-164.6335		-72.33608		-66.42	

AIC	235.96		341.27		158.67		144.84	
BIC	256.35		361.66		182.46		165.23	
B. Maximum dive duration ~ O2 index (M ^{0.163} for ectotherms; M ^{0.330} for endotherms) + Metabolic mode + Temperature + O2 index x Metabolic mode								
tree topology	star ($\lambda=0$)		time-calibrated branch lengths (no branchlength transformations)		Optimal Lambda ($\lambda=0.95$)		Optimal Rho ($\rho = 0.273$)	
	Estimate (\pm SE)	P-value	Estimate (\pm SE)	P-value	Estimate (\pm SE)	P-value	Estimate (\pm SE)	P-value
Intercept: ectothermy	2.4045 (\pm 0.160)	<0.0001	2.859 (\pm 1.968)	0.1477	2.009 (\pm 0.688)	0.0038	2.117 (\pm 0.257)	<0.0001
O2 index: ectothermy	1.211 (\pm 0.131)	<0.0001	1.906 (\pm 1.216)	0.1183	0.760 (\pm 0.620)	0.2283	0.967 (\pm 0.331)	0.0039
Metabolic mode: endothermy	-0.864 (\pm 0.227)	0.0002	-0.179 (\pm 1.312)	0.8918	-0.823 (\pm 0.483)	0.0895	-0.968 (\pm 0.321)	0.0029
Temperature	-1.068 (\pm 0.261)	0.0001	-1.938 (\pm 0.441)	<0.0001	-0.993 (\pm 0.328)	0.0027	-0.863 (\pm 0.289)	0.0031
O2 index x Metabolic mode: endothermy	-0.296 (\pm 0.178)	0.0984	0.915 (\pm 1.241)	0.4614	0.244 (\pm 0.646)	0.7062	0.015 (\pm 0.365)	0.9665
Log likelihood	-109.06		-161.71		-69.41		-63.5	
AIC	230.12		335.42		152.83		139.00	
BIC	250.5		355.81		176.61		159.39	
C. Maximum dive duration ~ O2 index (M ^{0.163} for ectotherms; M ^{0.330} for endotherms) + Metabolic mode + Temperature								
tree topology	star ($\lambda=0$)		time-calibrated branch lengths (no branchlength transformations)		Optimal Lambda ($\lambda=0.95$)		Optimal Rho ($\rho = 0.273$)	
	Estimate (\pm SE)	P-value	Estimate (\pm SE)	P-value	Estimate (\pm SE)	P-value	Estimate (\pm SE)	P-value
Intercept: ectothermy	2.199 (\pm 0.102)	<0.0001	2.461 (\pm 1.890)	0.1944	2.118 (\pm 0.617)	0.0007	2.122 (\pm 0.226)	<0.0001
O2 index	1.018 (\pm 0.062)	<0.0001	1.025 (\pm 0.229)	<0.0001	0.992 (\pm 0.125)	<0.0001	0.980 (\pm 0.122)	<0.0001
Metabolic mode: endothermy	-1.067 (\pm 0.192)	<0.0001	-0.157 (\pm 1.310)	0.9045	-0.820 (\pm 0.478)	0.0879	-0.967 (\pm 0.320)	0.0028
Temperature	-0.782 (\pm 0.197)	0.0001	-1.889 (\pm 0.435)	<0.0001	-1.018 (\pm 0.320)	0.0017	-0.866 (\pm 0.279)	0.0022
Log likelihood	-109.63		-163.12		-69.96		-63.41	
AIC	229.25		353.25		151.92		136.82	
BIC	246.27		336.24		172.34		153.83	