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2020-05-27

PROCEEDINGS OF THE ROYAL SOCIETY B

BIOLOGICAL SCIENCES

Universal metabolic constraints shape the evolutionary ecology of diving in animals.

| Journal: | Proceedings B |
|-------------------------------|---|
| Manuscript ID | RSPB-2020-0488.R1 |
| Article Type: | Research |
| Date Submitted by the Author: | n/a |
| Complete List of Authors: | Verberk, Wilco; Radboud Universiteit Nijmegen, Animal Ecology and Physiology Calosi, Piero; Université du Québec à Rimouski Brischoux, Francois; Université de La Rochelle, Centre d'Etudes Biologiques de Chizé Spicer, John; University of Plymouth Faculty of Science and Engineering, Garland, Jr., Theodore; University of California Riverside Bilton, David; Plymouth University, Marine Biology and Ecology Research Centre |
| Subject: | Ecology < BIOLOGY, Evolution < BIOLOGY, Physiology < BIOLOGY |
| Keywords: | allometry, ectothermy, endothermy, evolutionary physiology, paleophysiology, mass scaling |
| Proceedings B category: | Ecology |
| | |

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Author-supplied statements

Relevant information will appear here if provided.

Ethics

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Statement (if applicable): CUST_IF_YES_ETHICS :No data available.

Data

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Statement (if applicable):

We have made our data file publically available in Dryad. Note that this database in Dryad is private during for the duration of the article's peer review period. I have provided the pre-release preview and the csv file for the reviewers as supplementary files.

Conflict of interest

I/We declare we have no competing interests

Statement (if applicable): CUST_STATE_CONFLICT :No data available.

Authors' contributions

This paper has multiple authors and our individual contributions were as below

Statement (if applicable):

P.C. proposed the initial idea and together with D.T.B, J.I.S. and W.C.E.P.V. contributed to its development. F.B., P.C., and W.C.E.P.V. collated the data. W.C.E.P.V. led the data analysis with input from T.G. All authors discussed the results, and substantially contributed to the writing.

| 1 | Title: Universal metabolic constraints shape the evolutionary ecology of diving |
|-------------|---|
| 2 | in animals |
| 3 | Authors: Wilco C.E.P. Verberk ^{1,2} , Piero Calosi ^{2,3} , François Brischoux ⁴ , John I. Spicer ² , |
| 4 | Theodore Garland, Jr. ⁵ , David T. Bilton ^{2,6} |
| 5 6 7 | Affiliations: ¹ Department of Animal Ecology and Ecophysiology, Radboud University, P.O. Box 9010, 6500 GL Nijmegen, the Netherlands. |
| 8 | ² Marine Biology and Ecology Research Centre, School of Biological and Marine Sciences, |
| 9 | University of Plymouth, Drake Circus, Plymouth PL4 8AA, United Kingdom. |
| 10 | ³ Département de Biologie, Chimie et Géographie, Université du Québec à Rimouski, 300 |
| 11 | Allée des Ursulines, Rimouski, G5L 3A1, Québec, Canada. |
| 12 | ⁴ Centre d'Etudes Biologiques de Chizé, UMR 7372 CNRS-La Rochelle Université, 79360 |
| 13 | Villiers en Bois, France. |
| 14 | ⁵ Department of Evolution, Ecology, and Organismal Biology, University of California, |
| 15 | Riverside, CA 92521, USA. |
| 16 | ⁶ Department of Zoology, University of Johannesburg, PO Box 524, Auckland Park, 2006 |
| 17 | Johannesburg, South Africa. |
| 18 | * Corresponding author: Wilco Verberk. Radboud University, P.O. Box 9010, 6500 GL |
| 19 | Nijmegen, the Netherlands. Tel.: +31(0)243653155. E-mail: wilco@aquaticecology.nl |

20 Abstract:

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

35

36 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

40 Keywords:

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

42

44 Introduction

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

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

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

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

98

99 **Results**

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

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

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

136 **Discussion**

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

In the past, the relative paucity of data for ectotherm divers, has prevented rigorous 146 testing of the Oxygen Store/Usage Hypothesis across all diving animals. Our analyses 147 demonstrate that previous uncertainty regarding the scaling of dive duration with body mass in 148 ectotherms was a result of the lack of information on small ectotherm divers, and not because 149 ectotherms are more phylogenetically diverse than endotherms, or because they display greater 150 metabolic variation¹¹. In fact, the vertical scatter around the allometric relationships is similar for 151 152 ectotherms and endotherms. Such scatter shows that there is variation in diving capacity between species of similar size or phylogeny, highlighting that in particular lineages and species, body 153 mass and oxygen storage capacity may be uncoupled to some extent (Fig. 2A; see also^{11,13}). The 154 155 evolution of particular physiological adaptations may often explain such uncoupling. For example, the elevated hematocrit level found in marine snakes (Hydrophiinae) facilitates 156 157 increased aerobic dive duration⁴. Many diving mammals have evolved myoglobins with elevated 158 net surface charge, which facilitates higher intramuscular concentrations²⁴. Conversely, lungePage 9 of 30

feeding in balaenopterid rorquals is energetically costly and the evolution of lunge-feeding 159 appears to have compromised their diving capacities²⁵. Given the allometry of diving we report 160 here, such adaptations appear to be modulations superimposed upon the universal constraints of 161 size-dependent oxygen storage and utilisation. 162 Greater gains in dive capacity with body mass are predicted under the Oxygen 163 164 Store/Usage Hypothesis for endotherms, since their mass-specific rates of oxygen consumption decline more with increasing body mass compared to ectotherms¹, something which is supported 165 by empirical studies showing that scaling exponents for resting metabolic rate are lower for 166 endotherms than ectotherms^{19,20}. The mass-related differences between the dive duration of 167 ectotherms and endotherms reported here (Fig. 2A) are fully mirrored by mass-related 168 differences in their metabolic rates; not just in slopes, but also intercepts (Fig. 2B). Differences 169 in slopes disappeared when we accounted for differences in oxygen storage relative to usage, 170 using the index of oxygen storage capacity. The modelled slope for the oxygen index is close to 171 1, indicating a proportional relationship (Fig. 2B; Table 1), which makes sense as animals should 172 gain dive capacity in proportion to their capacity to store oxygen, once differences in oxygen 173 demand are accounted for. A sensitivity analysis, employing different scaling exponents for 174 175 ectotherm and endotherm metabolic rates (derived from a reanalysis of the largest database

available on these rates - see supplementary materials) yielded similar results (see Table S1). Our

demonstration of differences between ectotherms and endotherms in the mass scaling of dive

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

scaling. The maximum dive duration of endotherms and ectotherms converged at large body

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sizes, whereas there was no difference in scaling exponents when comparing endotherms and 182 ectotherms on the basis of index of oxygen storage capacity (Table 1, model B). Considering 183 differences in intercepts, for a given oxygen index, ectothermic divers such as reptiles can 184 remain submerged for much longer than their endothermic counterparts¹¹. Such greater dive 185 duration in ectotherms is partly related to their lower body temperature and partly to their 186 187 metabolic mode; effects of the latter accounting for a 10-fold difference in dive time (Model C, Table 1). This is in line with the observation that absolute metabolic rates are generally around 188 an order of magnitude lower in ectotherms compared to endotherms, when expressed at a 189 common temperature $^{26-28}$ - see also supplementary analysis. Although the largest ectotherms 190 approach the same dive duration as similarly sized endotherms, they will have smaller lower 191 oxygen consumption rates and concomitantly smaller oxygen stores. Oxygen stores scale 192 approximately isometrically with body mass, but the differences in metabolic scaling results in a 193 194 shallower mass scaling of dive duration in ectotherms, meaning that the benefits of ectothermy 195 for diving duration are reduced at large body sizes. Since temperature increases metabolic rate, higher temperatures result in lower dive 196

durations and as temperature has an exponential effect, stronger reductions are both expected and 197 198 observed towards higher body temperatures in endotherms (Fig. 2C). This non-linearity was encapsulated by our temperature correction factor, which expresses the effect temperature has on 199 200 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 temperature-driven increase in oxygen demand should translate to an equivalent reduction in 202 203 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

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

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

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

240

241 Materials and Methods

242 Data collection and selection

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

We focused on maximum dive duration as a proxy for the evolutionary limit to dive 250 capacity in a given species. Preliminary analyses showed that maximum dive duration co-varied 251 closely with mean dive duration (Fig. S2A), even after accounting for differences in body mass 252 and temperature (Fig. S2B). For species with multiple data entries for maximum dive duration, 253 we selected the entry closest to the 95th percentile, in an attempt to account for variation in 254 sample size across species⁴⁶. For species with many records, the absolute longest dive recorded 255 may also sometimes represent an extreme event, such as an animal being disoriented. Taking the 256 95th percentile will help to minimise the influence of such events. Temperature strongly affects 257 metabolic rate in ectotherms^{26, see also supplementary analysis}, and hence also affects dive duration (e.g. 258 ^{6,17,47,48}). Selection of the data entry closest to the 95th percentile for a given species was therefore 259 based on dive duration expressed at a common mean temperature, by correcting dive duration 260 with a (within-species) temperature correction factor: 261

262

263 Temperature correction factor = $e^{\frac{-Ea}{k}*(1/T_{emperature}-1/M_{ean temperature})}$

264

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

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

279

280 Data analyses

We explored the effect of body mass on dive duration using linear versions of phylogenetic 281 generalized least squares (PGLS) models. These models were used to test whether the mass 282 scaling of diving performance differed between ectotherms and endotherms, both in terms of 283 intercept, which would indicate absolute differences in dive capacity, and slope, which would 284 indicate differences in the mass dependence of diving performance. Both body mass and dive 285 286 duration were \log_{10} -transformed prior to analyses. In each model we tested for differences in the scaling exponent between ectotherms and endotherms by including an interaction term of body 287 mass x metabolic mode (i.e. ectotherm or endotherm). As temperature is known to affect dive 288 289 duration (see above), some variation in dive duration across species is likely attributable to differences in body temperature. Based on the Oxygen Store/Usage Hypothesis, such thermal 290 effects should be mediated through the effect temperature has on metabolic rate. To capture the 291 292 non-linear effect of temperature on metabolism, we calculated a temperature correction factor using the equation above, rather than including temperature directly. Preliminary analyses 293 294 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

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

³¹⁶ Under the *Oxygen Store/Usage Hypothesis*, an isometric increase in oxygen stores (M¹) 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 used to predict the positive scaling of fasting endurance with body mass⁵¹. In order to account for

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such mass related differences in metabolism, and test whether these differences in diving 320 allometry can be explained from known differences in metabolic scaling between ectotherms and 321 endotherms, we regressed dive duration against an index of oxygen storage capacity, instead of 322 body mass. This index of oxygen storage capacity is defined as: 323 324 O_2 index = $M^{1-\beta}$ 325 326 327 where β is the metabolic scaling exponent. Empirical evidence indicates that the metabolic scaling exponent differs between endotherms and ectotherms^{19,20}, which Glazier²¹ explained with 328 329 his 'metabolic-level boundaries hypothesis'. Consequently, this index was calculated based on their respective scaling exponents. Although many different exponents have been reported in the 330 literature, we considered the most applicable to be values that were phylogenetically corrected 331 and included weighted means with random effects (i.e. 0.837 for ectotherms and 0.670 for 332 endotherms)¹⁹. Moreover, these values for the scaling exponents align very closely with those 333 based on field metabolic rates reported in the same paper. We also ran a sensitivity analysis to 334 explore how different values for the scaling exponents observed in endotherms and ectotherms 335 influenced our analysis. The scaling exponents used for this were based on a re-analysis of 336 metabolic rates compiled from the literature⁵² and yielded similar results: when correcting for 337 differences in metabolic scaling we never found different slopes for ectotherms and endotherms. 338 Also, the model fitted a value for the oxygen index that was close to 1 (Table S1). 339 The correlation structure of PGLS models reflects the potential similarity of species' traits 340 resulting from shared evolutionary history and an assumed model of residual trait evolution (e.g., 341

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

would require good priors and may result in overfitting of the data. Consequently, we did not 365 pursue this approach further. Finally, we fitted an additional model that excluded the effects of 366 phylogeny: i.e. with $\lambda = 0$, which yields a star phylogeny and has one fewer parameter in the 367 model. 368 All analyses were performed in R, using the packages ape, picante, caper. Residual plots (Figs. 369 370 S5) were visually inspected for homoscedasticity, normality, and other assumptions. Effects of model variables are illustrated by means of partial residual plots using the package visreg. Partial 371 residual plots illustrate the relationship between the independent variable and a given response 372 variable whilst accounting for the effects of other independent variables in the model. Such plots 373 are constructed by adding the residuals of the model to the fitted relationship of the independent 374 variable of interest and plotting these values (on the y-axis) against the independent variable of 375 interest (on the x-axis). 376

377

378 Acknowledgments

We thank Leela Chakravarti and Fanny Vermandele for their assistance with manuscriptpreparation.

Funding: This study was initiated whilst PC was an RCUK Research Fellow, and WCEPV a
Marie-Curie Fellow with DTB at the University of Plymouth, and subsequently supported by
intramural funding from Radboud University and Université du Québec à Rimouski. WCEPV is
supported by a Marie Curie FP7 Integration Grant within the 7th European Union Framework
Programme (FP7-PEOPLE-2012-CIG proposal N° 334048), PC by an NSERC Discovery Grant
(RGPIN-2015-06500) and he is member of FRQNT-funded excellence research networks

| 387 | Québec-Ocean and QCBS. TG Jr was supported by an NSF grant and FB is supported by the |
|-----|--|
| 388 | CNRS. |
| 389 | Author contributions: P.C. proposed the initial idea and together with D.T.B, J.I.S. and |
| 390 | W.C.E.P.V. contributed to its development. F.B., P.C., and W.C.E.P.V. collated the data. |
| 391 | W.C.E.P.V. led the data analysis with input from T.G. All authors discussed the results, and |
| 392 | substantially contributed to the writing. |
| 393 | Competing interests: The authors declare no competing interests. |
| 394 | Data and materials availability: The dataset supporting this article have been uploaded to |
| 395 | Dryad: https://doi.org/10.5061/dryad.tqjq2bvv9. |
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| 520 | Supplementary Materials. |
| 338 | supprementary 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
- energies; 3) different transformations of the phylogenetic tree.
- 543 Figures S1-S4
- 544 Tables S1, S2
- 545 Image credits



Fig. 1. Phylogenetic tree of all species (N=226) used in the analyses, displaying maximum dive
duration (length of outer bars) and body mass (gradient in branch colours). Outer bars are colour
coded to represent Reptiles (purple), Mammals (green), Insects (orange), Birds (red) and

551 Amphibians (blue). For image credits see supplementary materials.





Fig. 2. Plots with all the data on maximum dive duration, colour coded for different groups of 555 animals (A), with 95% prediction intervals shown separately for ectotherms (in blue) and 556 endotherms (in red). Partial residual plots show how maximum dive duration (min) changes with 557 body mass (kg) (B), the index of oxygen storage capacity (C), and temperature (D), whereby 558 species are colour coded according to being ectotherms (blue) or endotherms (red). Note the 559 log₁₀ transformation for Dive duration, Body mass and the Oxygen index. Linear regression 560 equations are given in each plot (full details on the parameters can be found in Table 1). Partial 561 residual plots illustrate the relationship between the response variable (here maximum dive 562 duration) and a given independent variable whilst accounting for the effects of other independent 563 variables in the model. Hence variation in dive duration owing to differences in temperature is 564 accounted for in plot B and C, isolating the effects of body mass and the oxygen index 565 respectively, whereas plot D isolates the effects of temperature by accounting for differences in 566 body mass. For image credits see supplementary materials. 567

| 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
- 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 (λ=0) | | | time-calibrated branch lengths (no branchlength transformations) | | | Optimal Lambda (λ=0.95) | | | Optimal Rho (ρ = 0.273) | | |
| | Estimate (±SE) | P-value | | Estimate (±SE) | P-value | | Estimate (±SE) | P-value | | Estimate (±SE) | P-value | |
| Intercept: ectothermy | 2.405 (±0.160) | <0.0001 | | 2.859 (±1.968) | 0.1477 | | 2.009 (±0.688) | 0.0038 | | 2.117 (±0.257) | <0.0001 | |
| Body mass: ectothermy | 0.197 (±0.021) | <0.0001 | | 0.3106 (±0.198) | 0.1183 | | 0.124 (±0.102) | 0.2283 | | 0.158 (±0.054) | 0.0039 | |
| Metabolic mode: endothermy | -0.864 (±0.227) | 0.0002 | | -0.179 (±1.312) | 0.8918 | | -0.823 (±0.483) | 0.0895 | | -0.968 (±0.321) | 0.0029 | |
| Temperature | -1.068 (±0.261) | 0.0001 | | -1.938 (±0.441) | <0.0001 | | -0.993 (±0.328) | 0.0027 | | -0.863 (±0.289) | 0.0031 | |
| Body mass x Metabolic mode: endothermy | 0.105 (±0.041) | 0.0108 | | 0.016 (±0.214) | 0.9397 | | 0.207 (±0.112) | 0.0663 | | 0.167 (±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 | otor () =0 | \ | | time-calibrated branch | | | $O_{in}(t) = O_{in}(t) = O_{in}(t)$ | | | Optimal Disc (a = 0.072) | | |
| | star (A=0 |) | | transformations) | | | Optimai Lambda (x=0.95) | | | Optimar Kilo ($p = 0.273$) | | |
| | Estimate (±SE) | P-value | | Estimate (±SE) | P-value | | Estimate (±SE) | P-value | | Estimate (±SE) | P-value | |
| Intercept: ectothermy | 2.4045 (±0.160) | <0.0001 | | 2.859 (±1.968) | 0.1477 | | 2.009 (±0.688) | 0.0038 | | 2.117 (±0.257) | <0.0001 | |
| O2 index: ectothermy | 1.211 (±0.131) | <0.0001 | | 1.906 (±1.216) | 0.1183 | | 0.760 (±0.620) | 0.2283 | | 0.967 (±0.331) | 0.0039 | |
| Metabolic mode:endothermy | -0.864 (±0.227) | 0.0002 | | -0.179 (±1.312) | 0.8918 | | -0.823 (±0.483) | 0.0895 | | -0.968 (±0.321) | 0.0029 | |
| Temperature | -1.068 (±0.261) | 0.0001 | | -1.938 (±0.441) | <0.0001 | | -0.993 (±0.328) | 0.0027 | | -0.863 (±0.289) | 0.0031 | |
| O2 index x Metabolic mode: | -0.296 (±0.178) | 0.0984 | | 0.915 (±1.241) | 0.4614 | | 0.244 (±0.646) | 0.7062 | | 0.015 (±0.365) | 0.9665 | |
| endothermy | | | | | | | | | | | | |
| 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 ind | lex (M^0.163 for ecto | otherms; M | ^0.: | 330 for endotherms | s) + Metabol | ic r | node + Temperatur | e | | | | |
| tree topology | | | | time-calibrated | branch | | | | | | | |
| | star (λ=0) |) | | lengths (no branchlength | | | Optimal Lambda (λ=0.95) | | | Optimal Rho (ρ = 0.273) | | |
| | Estimate (+SE) | P-value | | transformat | ions) P-value | | Estimate (+SE) | P-value | | Estimate (+SE) | P-value | |
| Intercent: ectothermy | 2 199 (+0 102) | | | 2 461 (+1 890) | 0 1944 | | 2 118 (+0 617) | 0.0007 | | 2 122 (+0 226) | | |
| O2 index | 1.018 + (0.062) | <0.0001 | | 1.025 (+0.229) | < 0.0001 | | 0.992 + (0.125) | <0.0001 | | 0.980 (+0.122) | < 0.0001 | |
| Metabolic mode:endothermy | -1.067 (±0.192) | < 0.0001 | | -0.157 (±1.310) | 0.9045 | | -0.820 (±0.478) | 0.0879 | | -0.967 (±0.320) | 0.0028 | |
| Temperature | -0.782 (±0.197) | 0.0001 | | -1.889 (±0.435) | < 0.0001 | | -1.018 (±0.320) | 0.0017 | | -0.866 (±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 | | |