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Universal metabolic constraints shape the evolutionary ecology of diving in animals

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Diving as a lifestyle has evolved on multiple occasions when air-breathing terrestrial animals invaded the aquatic realm, and diving performance shapes the ecology and behaviour of all air-breathing aquatic taxa, from small insects to great whales. Using the largest dataset yet assembled, we show that maximum dive duration increases predictably with body mass in both 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 ectotherms. These differences in diving allometry can be fully explained by inherent differences between the two groups in their metabolic rate and how metabolism scales with body mass and temperature. Therefore, we suggest that similar constraints on oxygen storage and usage have shaped the evolutionary ecology of diving in all air-breathing animals, irrespective of their evolutionary history and metabolic mode. The steeper scaling relationship between body mass and dive duration in endotherms not only helps explain why the largest extant vertebrate divers 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.

1. Introduction

Diving behaviour has evolved independently many times in air-breathing animals as diverse as insects, amphibians, turtles, crocodiles, snakes, birds and mammals [1–6], as well as a number of extinct reptile lineages [7]. The behaviour and ecology of these air-breathers depend on their ability to remain submerged [8,9]. All diving animals face the same basic challenges, and natural selection generally should act to maximize dive duration within the constraints of an organism's morphology and physiology. Body mass has an overriding influence on maximum dive duration [10,11] and, according to the Oxygen Store/Usage Hypothesis [1,10,12], larger-bodied species should be better at 'holding their breath', because oxygen stores scale approximately isometrically ($m \sim 1$) with body mass, whereas oxygen requirements (metabolic rates) scale with negative allometry ($m < 1$). Owing to their lower mass-specific metabolic rates, large divers can store more oxygen relative to the rate at which they consume it. Support for this hypothesis is particularly strong for endotherms [10,13], although one recent study suggests it may also apply to ectotherms, albeit based on data limited to vertebrates [12]. A high metabolic rate is the main source of heat in endotherms, and their elevated metabolic rates while at rest enable them to maintain a relatively high and more-or-less constant internal temperature

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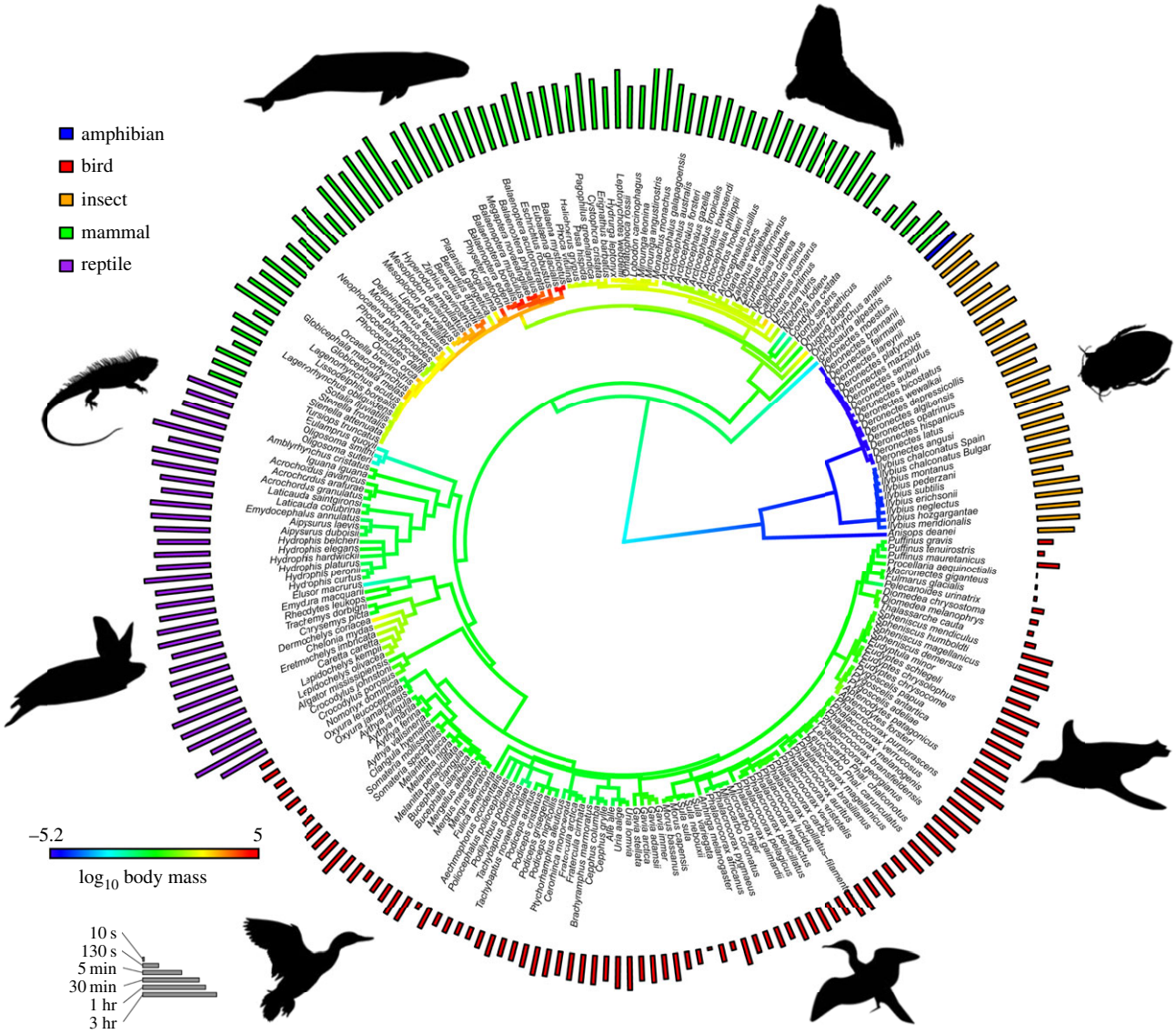

Figure 1. Phylogenetic tree of all species ($n = 226$) used in the analyses, displaying maximum dive duration (length of outer bars) and body mass (gradient in branch colours). Outer bars are colour coded to represent reptiles (purple), mammals (green), insects (orange), birds (red) and amphibians (blue). For image credits see the electronic supplementary material. (Online version in colour.)

(homeothermy) [14–16]. By this 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 temperatures (i.e. 'gigantothermy' and 'inertial homeothermy', such as the leatherback turtle *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 been hampered by the lack of empirical data for small-bodied taxa [11]. However, recent works [6,17] have generated data on the diving behaviour of 26 species of insects (figure 1), greatly broadening the phylogenetic representation and, most importantly, extending the body mass range of ectotherms available for analysis. In fact, these new data enable the comparative study of ectothermic animals ranging over approximately eight orders of magnitude in body mass, from small diving beetles (*Deronectes bicostatus* approx. 5.5 mg [17]) to large sea turtles (*Dermochelys coriacea* > 300 kg [18]). Drawing on the largest dataset compiled to date on dive duration and body mass in both ectotherm and endotherm divers, we test whether the Oxygen Store/Usage Hypothesis applies to all diving animals, irrespective of their evolutionary origin and metabolic mode. Specifically, we compiled and analysed 1792 records for 286 species, including 62 ectotherms and 224 endotherms. This represents increases of 78%, 121% and 10% for total number of records, ectotherm species and endotherm species, respectively, compared to the last update [12] (electronic supplementary material, figure S1A). To do so, we quantify the body mass dependence of maximum dive duration in both ectotherm and endotherm divers, and compare empirical scaling relationships of dive duration with the known mass dependency of metabolic rate (oxygen consumption) in the two groups (see Material and methods for more details on selection of appropriate scaling coefficients). Metabolic rate increases with body mass, but less strongly in endotherms than ectotherms, as reflected in scaling exponents for resting metabolic rate being lower for endotherms than ectotherms, both on empirical and theoretical grounds: see [19–21], Material and methods and the electronic

supplementary material analyses. Consequently, if the Oxygen Store/Usage Hypothesis holds true, scaling exponents for maximum dive duration should be smaller in ectotherms than endotherms, and this difference should be attributable to differences in metabolic scaling between the two groups [22]. Metabolic rate also increases with temperature and therefore we also included body temperature (where available) or water temperature in our analyses. Our working assumption is that diving in both ectotherms and endotherms is governed by the same general principles, meaning that differences in maximum dive duration should be mirrored by differences in metabolic rate, which is in turn related to differences in body mass and temperature. As a result, the lower oxygen requirements of ectotherms should enable them to remain submerged for longer than similarly sized endotherms [11], whereas the steeper metabolic scaling in ectotherms [19] should translate to smaller gains in diving performance with increasing body mass.

2. Results

Maximum dive duration varied from less than a minute in several birds to greater than 1 h in several turtle species and some cetaceans. Much of the variation in maximum dive duration can be accounted for by metabolic mode (endothermy versus ectothermy), body mass and temperature (table 1). The model best fitting the data employed phylogenetic generalized least squares (PGLS) based on a time-calibrated phylogenetic tree that was rescaled by Grafen's rho ($\rho = 0.273$). This model significantly outperformed a PGLS using a star phylogeny ($\lambda = 0$; ΔAkaike information criterion (ΔAIC) = 91.1) and a PGLS with a lambda close to 1 ($\lambda = 0.95$; Δ AIC = 13.8). Dive duration increased with body mass in both ectotherms and endotherms (figure 2*a*, $p < 0.021$), but scaling exponents differed significantly, with dive duration increasing more steeply with body mass in endotherms (body mass × metabolic mode interaction, $p = 0.022$). As an example, maximum dive duration increased almost 11-fold with a 1000-fold increase in body mass in endotherms, but only around threefold in ectotherms. In order to test whether these differences in diving allometry can be 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 index accounts for mass-related differences in oxygen usage and storage (see Material and methods). When substituting body mass for this index, we no longer found that dive duration scaled differently between ectotherms and endotherms (i.e. the interaction between the oxygen index and metabolic mode was non-significant; $p = 0.91$), the model without the interaction performing better (ΔAIC = 2.1; table 1 and figure 2*b*). Very similar results were obtained when rescaling the branches of the time-calibrated phylogeny using an estimated lambda ($\lambda = 0.95$) or when phylogeny was not incorporated (i.e. using a star phylogeny with $\lambda = 0$) (table 1).

We also found differences in intercepts (elevations) between ectotherms and endotherms; dive duration being greater in ectotherms than endotherms of comparable body mass (figure 2*a* and table 1). As differences in mass scaling complicate comparisons of intercepts, we based our exploration on the best fitting model employing the index of oxygen storage capacity (figure 2*b*; model C in table 1), meaning that such differences in scaling were accounted for. Based on that 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 was significantly affected by differences in temperature across species (table 1 and figure 2*c*). In all cases, the effect of the temperature correction factor was negative, meaning that the greater rate of oxygen consumption associated with elevated temperatures (see the electronic supplementary material, figure S3) resulted in a shorter dive duration. Because temperature exponentially increases metabolic rate, the effect of temperature is curvilinear (figure 2*c*) 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 demand would reduce dive duration by the same factor.

3. Discussion

Our work provides an unprecedented analysis of the physiological and evolutionary ecology of diving behaviour from a metabolic perspective that has far-reaching implications. We reveal clear differences in the mass scaling of maximum dive duration between ectotherms and endotherms and show that these different scaling relationships can be reconciled from known differences in 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 ectotherms has not evolved independently of body mass [11], and the same basic physiological principles have apparently shaped the evolutionary ecology of diving in all animals, from small diving beetles to great whales [11,12,17,23].

In the past, the relative paucity of data for ectotherm divers has prevented rigorous testing of the Oxygen Store/Usage Hypothesis across all diving animals. Our analyses demonstrate that previous uncertainty regarding the scaling of dive duration with body mass in ectotherms was a result of the lack of information on small ectotherm divers, and not because ectotherms are more phylogenetically diverse than endotherms, or because they display greater metabolic variation [11]. In fact, the vertical scatter around the allometric relationships is similar for 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 mass and oxygen storage capacity may be uncoupled to some extent (figure 2*a*; see also [11,13]). The evolution of particular physiological adaptations may often explain such uncoupling. For example, the elevated haematocrit level found in marine snakes (Hydrophiinae) facilitates increased aerobic dive duration [4]. Many diving mammals have evolved myoglobins with elevated net surface charge, which facilitates higher intramuscular concentrations [24]. Conversely, lunge-feeding in balaenopterid rorquals is energetically costly and the evolution of lunge-feeding appears to have compromised their diving capacities [25]. Given the allometry of diving we report here, such adaptations appear to be modulations superimposed upon the universal constraints of size-dependent oxygen storage and use.

Greater gains in dive capacity with body mass are predicted under the Oxygen Store/Usage Hypothesis for endotherms, because their mass-specific rates of oxygen consumption decline more with increasing body mass compared to

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

	star ($\lambda = 0$)		time-calibrated branch lengths (no branch length transformations)		optimal lambda ($\lambda = 0.95$)		optimal rho ($\rho = 0.273$)	
tree topology	estimate (±s.e.)	*p*-value	estimate (±s.e.)	*p*-value	estimate (±s.e.)	*p*-value	estimate (±s.e.)	*p*-value
A. maximum dive duration∼body mass + metabolic mode + temperature + body mass × metabolic mode								
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 × 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	−111.98		−164.63		−72.34		−66.42	
AIC	235.96		341.27		158.67		144.84	
BIC	256.35		361.66		182.46		165.23	
B. maximum dive duration∼O_2 index ($M^{0.163}$ for ectotherms; $M^{0.330}$ for endotherms) + metabolic mode + temperature + O_2 index × metabolic mode								
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
o_2 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
o_2 index × metabolic mode: endothermy	−0.296 (±0.178)	0.0984	0.915 (±1.241)	0.4614	0.244 (±0.646)	0.7062	0.015 (±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 ∼ O_2 index ($M^{0.163}$ for ectotherms; $M^{0.330}$ for endotherms) + metabolic mode + temperature								
intercept: ectothermy	2.199 (±0.102)	<0.0001	2.461 (±1.890)	0.1944	2.118 (±0.617)	0.0007	2.122 (±0.226)	<0.0001
O_2 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	

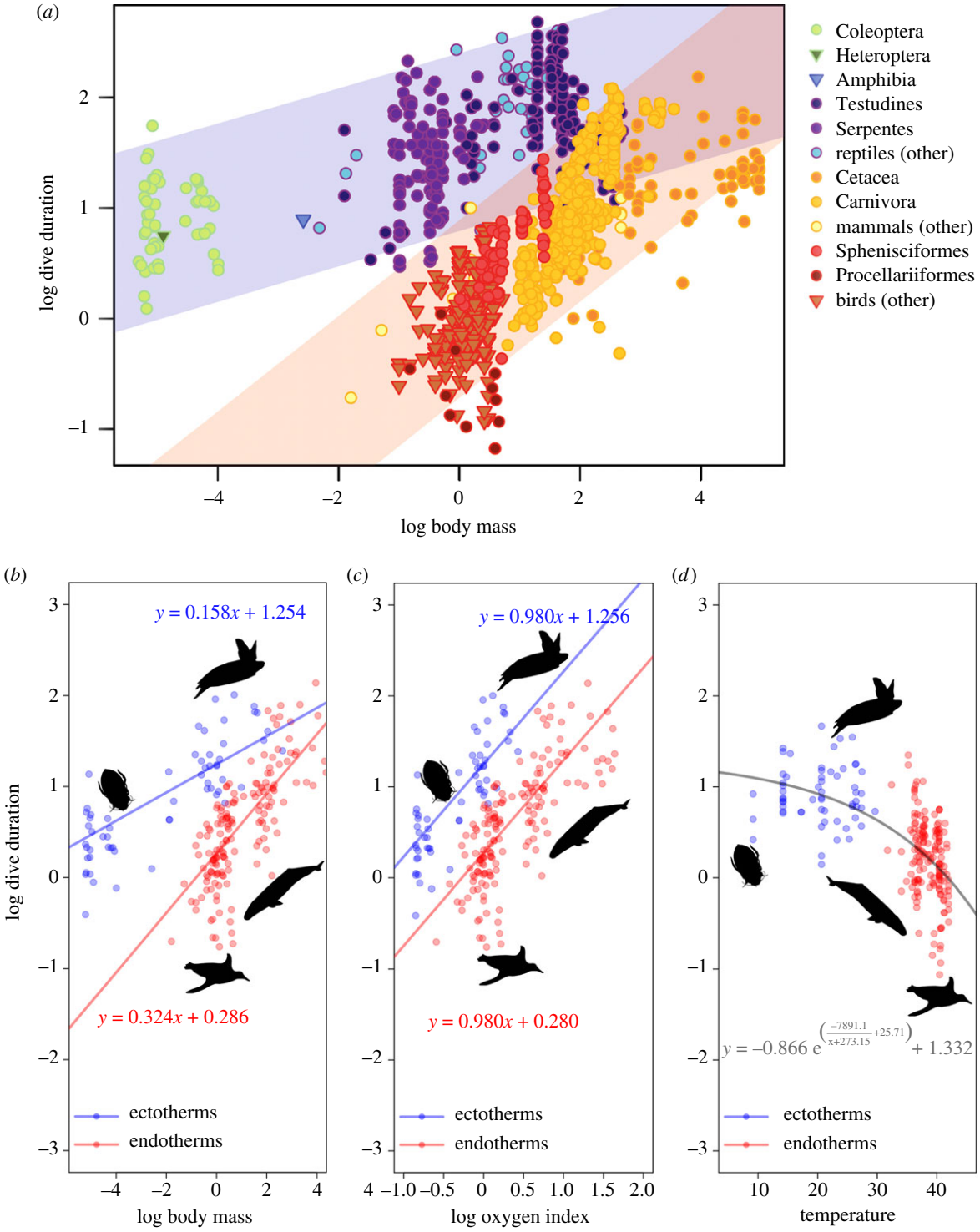

Figure 2. Relationship between maximum dive duration and body mass, colour coded for different groups of animals (*a*), with 95% prediction intervals shown separately for ectotherms (in blue) and endotherms (in red). Partial residual plots show how maximum dive duration (min) changes with body mass (kg) (*b*), the index of oxygen storage capacity (*c*), and temperature (*d*), whereby species are colour coded according to being ectotherms (blue) or endotherms (red). Note the $\log_{10}$ transformation for dive duration, body mass and the oxygen index. Linear regression equations are given in each plot (full details on the parameters can be found in table 1). Partial residual plots illustrate the relationship between the response variable (here maximum dive duration) and a given independent variable while accounting for the effects of other independent variables in the model. Hence variation in dive duration owing to differences in temperature is accounted for in plots (*b*) and (*c*), isolating the effects of body mass and the oxygen index respectively, whereas plot (*d*) isolates the effects of temperature by accounting for differences in body mass. For image credits see the electronic supplementary material. (Online version in colour.)

ectotherms, something which is supported by empirical studies showing that scaling exponents for resting metabolic rate are lower for endotherms than ectotherms [19–22]. The mass-related differences between the dive duration of ectotherms and endotherms reported here (figure 2*a*) are fully mirrored by mass-related differences in their metabolic rates; not just in slopes, but also intercepts (figure 2*b*). Differences in slopes disappeared when we accounted for differences in oxygen storage relative to usage, using the index of oxygen storage capacity. The modelled slope for the oxygen index is close to 1, indicating a proportional relationship (figure 2*b* and table 1), which makes sense as animals should gain dive capacity in proportion to their capacity to store oxygen, once differences in oxygen demand are accounted for. A sensitivity

analysis, employing different scaling exponents for ectotherm and endotherm metabolic rates (derived from a reanalysis of the largest database available on these rates—see the electronic supplementary material) yielded similar results (see the electronic supplementary material, table S1). Our demonstration of differences between ectotherms and endotherms in the mass scaling of dive duration contrasts with previous analyses, limited to vertebrates [12], that did not find such differences. The greater range of animal body sizes in our study, including larger (leatherback turtles) and smaller (dytiscid beetles) ectotherms, probably enabled us to detect these differences in scaling. The maximum dive duration of endotherms and ectotherms converged at large body sizes, whereas there was no difference in scaling exponents when comparing endotherms and ectotherms on the basis of index of oxygen storage capacity (table 1, model B). Considering differences in intercepts, for a given oxygen index, ectothermic divers such as reptiles can remain submerged for much longer than their endothermic counterparts [11]. Such greater dive duration in ectotherms is partly related to their lower body temperature and partly to their metabolic mode; effects of the latter accounting for a 10-fold difference in dive time (table 1, model C). This is in line with the observation that absolute metabolic rates are generally around an order of magnitude lower in ectotherms compared to endotherms, when expressed at a common temperature [26–28]—see also the electronic supplementary material analysis. Although the largest ectotherms approach the same dive duration as similarly sized endotherms, they will have smaller lower oxygen consumption rates and concomitantly smaller oxygen stores. Oxygen stores scale approximately isometrically with body mass, but the differences in metabolic scaling results in a shallower mass scaling of dive duration in ectotherms, meaning that the benefits of ectothermy for diving duration are reduced at large body sizes.

Because temperature increases metabolic rate, higher temperatures result in lower dive durations and as temperature has an exponential effect, stronger reductions are both expected and observed towards higher body temperatures in endotherms (figure 2*c*). This nonlinearity was encapsulated by our temperature correction factor, which expresses the effect temperature has on oxygen demand, relative to a reference temperature (see the electronic supplementary material, figure S3). As such, it represents a 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 dive duration. As dive duration on a $\log_{10}$ scale also represents a multiplication factor, the 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 20–30× more oxygen than water, is less viscous and less dense and consequently rates of oxygen diffusion are approximately 300 000 times faster in air than in water [29,30]. Large animals are, therefore, much better able to meet their metabolic demands by breathing air rather than obtaining oxygen from water, which could partly explain why the largest aquatic animals to have evolved are air-breathing divers rather than fishes [31]. Today, the largest diving animals are all true endotherms (Cetacea). Although endothermy in itself is not a prerequisite to be a good diver, it may have facilitated the evolution of large body size. Recent studies of bone and soft tissue anatomy [7,32–34], as well as the oxygen isotope composition of tooth phosphate [35,36], suggest that ichthyosaurs, pleisiosaurs and mososaurs, and perhaps some other extinct marine reptile groups, were also truly endothermic. As well as allowing increased aerobic capacity [14,37], endothermy facilitates the colonization of a wide range of marine habitats, including relatively cold seas, known to have been occupied by such marine reptiles [35,38]. Although the fossil record of these taxa is punctuated by extinction events which reduce morphological diversity (e.g. [39]), all three groups contain species that achieved very large body sizes, in some cases comparable to some of the largest modern cetaceans [40], and show evidence of increases in body size with time [39,41,42]. Because the scaling exponents for metabolic rate are lower for endotherms when compared to ectotherms, net gains in dive duration *per* unit mass increase are greater in endothermic animals. Although many other factors clearly influence body size, this extra advantage of being large may, at least in part, have facilitated the evolution of large body size in both extinct and extant tetrapod divers.

At the macroevolutionary level, once differences in metabolic rate are accounted for, both endothermic and ectothermic animals converge on the same allometric relationship when 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 evolutionary history. Viewed through the lens of the Oxygen Store/Usage Hypothesis, body mass and temperature affect dive duration in a similar manner in taxa as evolutionarily distant as insects, reptiles, birds and mammals. Consequently, the same general physical and physiological principles have shaped the evolution of diving in all animal groups, both ancient and modern, constituting a new fundamental principle for evolutionary physiology [43,44].

4. Material and methods

(a) 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 & Kovacs [3] 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 1792 records for 286 species of which 62 were ectotherms and 224 endotherms (figure 2*a*; [46]).

We focused on maximum dive duration as a proxy for the evolutionary limit to dive capacity in a given species. Preliminary analyses showed that maximum dive duration covaried closely with mean dive duration (electronic supplementary material, figure S2A), even after accounting for differences in body mass and temperature (electronic supplementary material, figure S2B). For species with multiple data entries for maximum dive duration, we selected the entry closest to the 95th percentile, in an attempt to account for variation in sample size across species [47]. For species with many records, the absolute longest dive recorded may also

sometimes represent an extreme event, such as an animal being disoriented. Taking the 95th percentile will help to minimize the influence of such events. Temperature strongly affects metabolic rate in ectotherms [26], see also the electronic supplementary material analysis, and hence also affects dive duration (e.g. [6,17,48,49]). Selection of the data entry closest to the 95th percentile for a given species was therefore based on dive duration expressed at a common mean temperature, by correcting dive duration with a (within-species) temperature correction factor:

$$\text{temperature correction factor} = e^{-\frac{-Ea}{k} \times \left(\frac{1}{\text{temperature}} - \frac{1}{\text{mean temperature}}\right)},$$

where Ea is the activation energy in eV and k is the Boltzmann constant in eV K^{-1} and temperature is expressed in Kelvin. Here, we used an Ea of 0.68 eV, which roughly equates to a Q_{10} of 2.4, as is typically found in intraspecific comparisons (see the electronic supplementary material). Temperature values refer to body temperature where available (all endotherms and some ectotherms) and otherwise to water temperature (most ectotherms). The common mean temperature represented the mean across all species in the database (33°C); at this mean temperature the temperature correction factor = 1. By selecting the data entry of the individual whose dive duration was closest to the 95th percentile (see above), we assembled data on body 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 the electronic supplementary material, figure S1B). We excluded the very high submergence times (greater than 30 000 min) reported for the Fitzroy river turtle, *Rheodytes leukops*, because 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 bursae [50].

(b) Data analyses

We explored the effect of body mass on dive duration using linear versions of PGLS models. These models were used to test whether the mass scaling of diving performance differed between ectotherms and endotherms, both in terms of intercept, which would indicate absolute differences in dive capacity, and slope, which would indicate differences in the mass dependence of diving performance. Both body mass and dive 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 mass × metabolic mode (i.e. ectotherm or endotherm). As temperature is known to affect dive duration (see above), some variation in dive duration across species is probably attributable to differences in body temperature. Based on the Oxygen Store/Usage Hypothesis, such thermal effects should be mediated through the effect temperature has on metabolic rate. To capture the nonlinear effect of temperature on metabolism, we calculated a temperature correction factor using the equation above, rather than including temperature directly. Preliminary analyses confirmed that models which employed this correction factor were better supported than those using raw temperatures. Because we are making across-species comparisons here, we employed the activation energy reported for interspecific comparisons (i.e. Ea = 0.43 eV [51]; electronic supplementary material, figure S3), which roughly corresponds to a Q_{10} of 1.7. Although it is well established that thermal activation energies differ when making comparisons across or within species, we also ran sensitivity analyses to determine whether our conclusions were robust to different values for activation energy. These analyses yielded similar results for both 25% lower and 25% higher activation energies (see the electronic supplementary material, 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 difference in dive allometry between ectotherms and endotherms. Preliminary analyses also explored whether ectotherms and endotherms differed in the thermal sensitivity of their dive durations, by including an interaction between metabolic mode and the temperature correction factor. However, such models were uninformative, as endotherms and ectotherms differed both with respect to body mass and body temperature, making it impossible to disentangle the relative importance of these parameters when both are allowed to vary. Birds, with their relatively low dive durations, are both smaller and warmer compared to mammals. Similarly, endotherms are both larger and warmer than ectotherms. Owing to this covariation between body size and body temperature across clades, we calculated the thermal effect on metabolism using the same activation energy across all species (see the electronic supplementary material, figure S3), rather than fitting them separately in the models. Studies that investigate the thermal sensitivity of metabolic rate in ectotherms suggest that although species differ, a single value for activation energy can approximate the thermal sensitivity in large-scale comparisons [23], including in the context of diving [12].

Under the Oxygen Store/Usage Hypothesis, an isometric increase in oxygen stores (M^1) and a suballometric increase in metabolism (M^β, with $\beta < 1$) generate an increase in oxygen 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 mass [52]. In order to account for such mass related differences in metabolism, and test whether these differences in diving allometry can be 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 index of oxygen storage capacity is defined as

$$O_2 \text{ index} = M^{1-\beta},$$

where β is the metabolic scaling exponent. Empirical evidence indicates that the metabolic scaling exponent differs between endotherms and ectotherms [19–22], which Glazier [22] explained with 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 literature, we considered the most applicable to be values that were phylogenetically corrected and included weighted means with random effects (i.e. 0.837 for ectotherms and 0.670 for endotherms) [19]. Moreover, these values for the scaling exponents align very closely with those based on field metabolic rates reported in the same paper. We also ran a sensitivity analysis to explore how different values for metabolic scaling exponents observed in endotherms and ectotherms influenced our analysis. The metabolic scaling exponents used for the sensitivity analysis were based on a re-analysis of resting metabolic rates compiled from the literature [53] and yielded similar results: when correcting for differences in metabolic scaling we never found different slopes for mass scaling of dive duration between ectotherms and endotherms. Also, the model fitted a value for the oxygen index that was close to 1 (electronic supplementary material, table S1).

The correlation structure of PGLS models reflects the potential similarity of species' traits resulting from shared evolutionary history and an assumed model of residual trait evolution (e.g. [54–56]). These models can incorporate a transformation parameter that, in essence, stretches the internal nodes of the tree either towards the tips of the tree (implying more phylogenetic signal in the residual trait values) or towards the root of the tree (implying less phylogenetic signal in the residuals). Given that we compare animals as different as turtles and diving beetles, accounting for the influence of phylogeny is not straightforward. Therefore, we have considered different transformation

parameters and compared their goodness of fit (see the electronic supplementary material, figure S4). One such transformation parameter is Pagel's lambda (λ) [57]. A value for lambda close to zero indicates low phylogenetic signal (phylogenetic independence between species' residuals, or a star phylogeny), while a value closer to one suggests that species' traits evolved randomly through evolutionary timescales via a process similar to Brownian motion. It is also possible to scale branches differently, depending on the position relative to the root by using Grafen's [58] rho (ρ). For values of ρ near 0, branches near the tips are expanded, while for values above 1, branches near the root are compressed, and vice versa. We constructed a topological tree for all species in our dataset, drawing on published phylogenies [59–63] (figure 1) and added branch length estimates using TimeTree [64]. We then considered transformation effects of either Pagel's lambda (λ) or Grafen's rho (ρ) and compared the goodness of fits (table 1). Both transformation effects had a clear optimum (electronic supplementary material, figure S4), which significantly improved upon the non-phylogenetic analysis (λ) and the untransformed time calibrated tree ($\lambda = 1$) (table 1). We also considered Ornstein–Uhlenbeck (OU) models, in the ape and nlme packages. While these fitted the data (alpha = 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 attractor in our models: e.g. beetles and whales are unlikely to share a common optimal body size. While 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 pursue this approach further. Finally, we fitted an additional model that excluded the effects of phylogeny: i.e. with $\lambda = 0$, which yields a star phylogeny and has one fewer parameter in the model.

All analyses were performed in R, using the packages ape, picante, caper. Residual plots (electronic supplementary material, figure 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 residual plots illustrate the relationship between the independent variable and a given response variable while accounting for the effects of other independent variables in the model. Such plots are constructed by adding the residuals of the model to the fitted relationship of the independent variable of interest and plotting these values (on the y-axis) against the independent variable of interest (on the x-axis).

Data accessibility. The dataset supporting this article have been uploaded to Dryad: https://dx.doi.org/10.5061/dryad.tqjq2bvv9 [46].

Authors' contributions. 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.

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