Common metabolic constraints on dive duration in endothermic and ectothermic vertebrates

April Hayward[1], Mariela Pajuelo[1], Catherine G. Haase[2], David M. Anderson[1] and James F. Gillooly[1]

[1] Department of Biology, University of Florida, Gainesville, FL, USA
[2] School of Natural Resources and Environment, University of Florida, Gainesville, FL, USA

ABSTRACT

Dive duration in air-breathing vertebrates is thought to be constrained by the volume of oxygen stored in the body and the rate at which it is consumed (i.e., "oxygen store/usage hypothesis"). The body mass-dependence of dive duration among endothermic vertebrates is largely supportive of this model, but previous analyses of ectothermic vertebrates show no such body mass-dependence. Here we show that dive duration in both endotherms and ectotherms largely support the oxygen store/usage hypothesis after accounting for the well-established effects of temperature on oxygen consumption rates. Analyses of the body mass and temperature dependence of dive duration in 181 species of endothermic vertebrates and 29 species of ectothermic vertebrates show that dive duration increases as a power law with body mass, and decreases exponentially with increasing temperature. Thus, in the case of ectothermic vertebrates, changes in environmental temperature will likely impact the foraging ecology of divers.

Subjects Animal Behavior, Ecology, Marine Biology, Zoology
Keywords Diving behavior, Metabolic theory, Metabolism, Thermal ecology, Oxygen storage, Allometry, Scaling

INTRODUCTION

The length of time that air-breathing vertebrate divers can remain submerged is an important constraint on their foraging activities, and perhaps ultimately on their fitness (*Butler & Jones, 1982*; *Kooyman, 1989*; *Stephens et al., 2008*; *Andrews & Enstipp, in press*). Consequently, vertebrates display a wide variety of behavioral, morphological, and physiological adaptations to enhance dive capacity. For example, endothermic vertebrates that dive show a relatively high capacity to store oxygen, use anaerobic metabolism, and reduce oxygen demand in non-vital tissues to prolong dive duration (*Boyd, 1997*; *Butler & Jones, 1997*; *Kooyman & Ponganis, 1998*). With respect to oxygen storage, cetaceans have higher densities of myoglobin in their tissues of a molecular form that has evolved to be more stable at depth (*Mirceta et al., 2013*). Despite such specialization, maximum dive duration in endotherms varies somewhat predictably with body mass based on the amount of oxygen stored in the body and the rate at which oxygen is consumed (*Butler & Jones, 1982*; *Schreer & Kovacs, 1997*; *Halsey, Blackburn & Butler, 2006*; *Halsey, Butler & Blackburn, 2006*; *Stephens et al., 2008*). However, the extent to which dive duration

may similarly vary with body mass in ectotherms as predicted by the oxygen store/usage hypothesis is less clear. Recent studies concluded that ectotherms fail to conform to expectations, and attributed this to ectotherms possessing characteristics that weaken any allometric constraints associated with diving (e.g., the ability to use aquatic respiration to supplement oxygen stores, and to enter thermally-induced hypo-metabolic states, to extend dives) (*Brischoux et al., 2008*; *Campbell et al., 2010*). In the case of aquatic respiration, some air-breathers may respire in water using lungs, whereas others may respire through their integument (i.e., "cutaneous respiration"; *Lenfant & Johansen, 1972*; *Feder & Burggren, 1985*). Yet, the potentially confounding effects of temperature on oxygen consumption rates and thus dive duration have not yet been examined in vertebrate ectotherms.

Here we present broad-scale analyses of dive duration in both endothermic and ectothermic vertebrates. We compare the predicted body mass and temperature dependence of dive duration based on the oxygen store/usage hypothesis to analyses of extensive empirical data compiled from the literature. The model and results presented here build on previous work in endotherms (*Butler & Jones, 1982*; *Kooyman, 1989*; *Stephens et al., 2008*) to examine the relationship in ectotherms, particularly with respect to temperature.

We begin by examining the predicted body mass and/or temperature dependence of dive duration based on the oxygen store/usage hypothesis. This hypothesis stipulates that dive duration (t_D) is a function of the total amount of oxygen carried by an organism on its dive (TO_2) divided by the rate at which that oxygen is used (i.e., its metabolic rate, B) (*Butler & Jones, 1982*; *Kooyman, 1989*). Thus,

$$t_D = TO_2/B \tag{1}$$

where oxygen storage capacity scales approximately linearly with body mass (M) and is independent of temperature (*Lindstedt & Calder III, 1981*; *Stephens et al., 2008*; *Campbell et al., 2010*) such that:

$$TO_2 = aM^1, \tag{2}$$

where a is a constant that describes the amount of oxygen that can be stored per gram of body mass (*Lindstedt & Calder III, 1981*; *Campbell et al., 2010*). Oxygen consumption rate in Eq. (1), however, has both a body mass and temperature dependence such that:

$$B = c \cdot M^d \cdot e^{0.12Tc}, \tag{3}$$

where c is a constant describing the amount of oxygen consumed per unit body mass, d describes the scaling of whole organism oxygen consumption rate with body mass (M), and $e^{0.12Tc}$ describes the exponential temperature dependence of oxygen consumption rate that is roughly equivalent to a Q_{10} of 2.5 (*Charnov & Gillooly, 2003*). Thus, we expect that the oxygen store/usage hypothesis should have both a body mass and temperature dependence such that:

$$t_D = a \cdot c^{-1} \cdot M^{b-d} \cdot e^{-0.12Tc}. \tag{4}$$

Note that the body mass dependence of oxygen consumption rate may differ between endotherms and ectotherms (*Gilloly et al., 2016*), and thus the body mass dependence of dive duration may also differ. Still, the scaling exponent for whole organism oxygen consumption rate shown in Eq. (4) (i.e., "*d*") is expected to be close to a value of 3/4 (*Isaac & Carbone, 2010*) and thus considerably less than the scaling exponent for oxygen storage (i.e., "*b*") of roughly 1. The effect of temperature on oxygen consumption rate, though, appears to be more similar in both groups (*Gilloly et al., 2001*). We evaluate the body mass and temperature dependence of dive duration from Eq. (4) for a diverse assortment of mammals, birds, reptiles, and amphibians (Appendix S1).

METHODS

Data collection

Data on median and maximum dive duration, body mass, and temperature were obtained from previously published studies for 181 species of endotherms and 29 species of ectotherms (Appendix S1). Leatherback turtles (*Dermochelys coriacea*) were excluded from consideration since they are functionally endothermic (*Penick et al., 1998*; *Southwood et al., 2005*; *Bostrom & Jones, 2007*), and direct measures of body temperature were not available. The body temperature of this species may be as much as 18 °C higher than ambient temperatures (*Frair, Ackman & Mrosovsky, 1972*).

For ectotherms, we used direct measures of body temperature when available, but otherwise we used ambient environmental temperatures as a proxy for body temperatures. For endotherms, we used species-specific measures of body temperatures for mammals and birds when available, or the mean body temperature of species from the same genus (*Clarke & Rothery, 2008*). If both of these estimates were not available, we used the mean body temperatures of birds (41.5 °C) and mammals (37 °C) (*Clarke & Rothery, 2008*) (Appendix S1). For body mass, we used the values of study subjects, or if unavailable, estimates of adult body masses from other sources (Appendix S1).

Analyses

We evaluated the body mass and temperature dependence of median and maximum dive duration using Bayesian generalized linear mixed-models (*Lunn et al., 2000*; *Bolker et al., 2009*) implemented in R package *MCMCglmm* (*Hadfield, 2010*). In performing these analyses, we accounted for any non-independence due to shared evolutionary history by including a vertebrate supertree recently constructed by *Gilloly et al. (2016)*, and by treating species as a random effect. This approach also accounted for effects of species sample sizes. To evaluate statistical models, we calculated conditional R^2 values for each model (*Nakagawa & Schielzeth, 2013*), and assessed model assumptions using diagnostic tests associated with phylogenetic analyses (*Paradis, Claude & Strimmer, 2004*; *Kembel et al., 2010*).

To best assess the temperature-dependence of median and maximum dive duration, we first performed analyses on the entire dataset. This dataset includes individuals of the same species measured at different temperatures. To best assess the mass-dependence of dive duration, we performed an additional set of analyses that was largely restricted to one point per species except when body mass differed substantially between males or females

Table 1 **Body mass and temperature dependence of dive duration in vertebrates.** Outputs from generalized linear mixed-models relating dive duration (median or maximum, in minutes) to body mass (natural log-transformed, in grams) and temperature (°C). Conditional R^2 values are reported, along with the slopes and intercepts of the relationships, and the sample sizes (N; with number of species). Results shown here represent the full dataset with multiple individuals for many species.

Group	Resp. Var.	Intercept (95% CI)	ln(Mass) (95% CI)	Temp. (95% CI)	R^2	N (species)
Ectotherms	Med.	4.00 (1.78,5.83)	0.19 (0.06,0.32)	−0.13 (−0.16,−0.09)	0.72	267 (29)
	Max.	5.88 (3.42,8.21)	0.09 (−0.09,0.26)	−0.11 (−0.13,−0.09)	0.81	267 (29)
Endotherms	Med.	−1.65 (−7.51,3.79)	0.42 (0.35,0.49)	−0.06 (−0.20,0.08)	0.72	738 (181)
	Max.	0.52 (−4.71,6.37)	0.34 (0.30,0.42)	−0.07 (−0.21,0.07)	0.62	738 (181)
All	Med.	2.34 (0.94,3.82)	0.37 (0.31,0.42)	−0.14 (−0.16,−0.11)	0.38	1,005 (210)
	Max.	3.34 (1.98,4.56)	0.32 (0.27,0.38)	−0.12 (−0.14,−0.10)	0.28	1,005 (210)

of a species, or between juveniles and adults. For this second set of analyses, median and maximum dive durations were normalized to 30 °C for all species by assuming a Q_{10} of 2.5 for oxygen consumption rate (*Gillooly et al., 2001*; *White, Phillips & Seymour, 2006*).

RESULTS AND DISCUSSION

Results show support for the body mass and temperature dependence of dive duration predicted by the oxygen store/usage hypothesis (*Butler & Jones, 1982*; *Kooyman, 1989*; Eq. (4)). With respect to body mass, analysis of the full dataset showed that median and maximum dive duration increased as a power law with body mass in both ectothermic and endothermic vertebrates (Table 1). While scaling exponents varied from 0.09–0.42 depending on the group in question, for ectotherms the 95% confidence intervals of these scaling exponents included the 0.25 one would expect for dive duration (Table 1; Eq. (4)) based on the linear scaling of oxygen storage and a 3/4 power scaling of oxygen consumption rate (*Isaac & Carbone, 2010*; *Gillooly et al., 2016*; but see *White, Phillips & Seymour, 2006*). In the case of endotherms, however, the confidence limits of these analyses did not include 3/4 (but did include 2/3; Table 1). Still, when the dataset was restricted largely to one point per species, and adjusted to a common temperature, the scaling exponents for median and maximum dive duration ranged from only 0.21 to 0.34, in closer agreement with expectations from the oxygen store/usage hypothesis and the 3/4 scaling of oxygen consumption (Table 2; Eq. (4)). With respect to ectotherms, then, our results differ from previous studies showing no body mass dependence of dive duration (*Brischoux et al., 2008*; *Campbell et al., 2010*). We speculate that this is because we explicitly accounted for the effects of temperature.

A comparison of the body mass-dependence of dive duration in endothermic and ectothermic vertebrates shows both similarities and differences-both of which are qualitatively consistent with the oxygen store/usage hypothesis. First, body mass explained between 63–68% in temperature-adjusted median and maximum dive duration in both groups. However, the scaling exponents for these relationships in ectotherms (0.21, 0.22) were slightly lower than those of endotherms (0.31, 0.34; Fig. 1 and Table 2). This observation is consistent with work showing that the body mass scaling of oxygen consumption rate is steeper in ectotherms (exponents: 0.84–0.90) than in endotherms (0.70–0.74)

Table 2 **Body mass dependence of temperature-adjusted dive duration in vertebrates.** Outputs from generalized linear mixed-models relating temperature-adjusted dive duration (median or maximum) to body mass (ln-transformed, in grams) for ectothermic (amphibians and reptiles) and endothermic (mammals and birds) vertebrates. Conditional R^2 values are reported, along with the slopes and intercepts of the relationships, and sample sizes (N; with number of species).

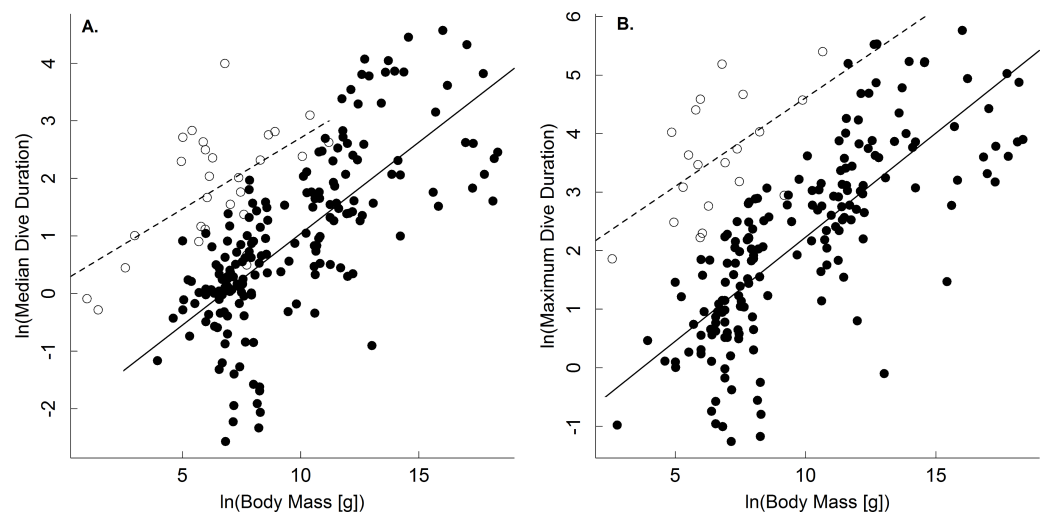| Group	Res. Var	Intercept (95%)	ln(Mass) (95% CI)	R^2	N (species)
Ectotherms	Med.	0.12 (−1.88,2.34)	0.22 (0.02,0.42)	0.68	28 (28)
	Max.	2.05 (−2.26,6.36)	0.21 (−0.08,0.55)	0.67	28 (28)
Endotherms	Med.	−2.49 (−3.94,−0.90)	0.34 (0.23,0.42)	0.63	187 (165)
	Max.	−1.02 (−2.51,0.42)	0.31 (0.24,0.39)	0.68	187 (165)
All	Med.	−1.47 (−2.72,−0.26)	0.30 (−0.21,0.41)	0.33	215 (193)
	Max.	0.02 (−1.30,1.57)	0.31 (0.22,0.42)	0.22	215 (193)

Figure 1 **The body mass dependence of dive duration in vertebrates.** The natural logarithm of median (A) and maximum dive duration (min.; B) as a function of the natural logarithm of body mass (g) for air-breathing endothermic (birds and mammals; closed points, solid line) and ectothermic vertebrates (reptiles and amphibians; open points, dashed line). Data were normalized to 30 °C assuming a Q_{10} of 2.5. Most points represent a single species (see 'Methods,' and Table 2 for statistics).

(*Gillooly et al., 2016*). Similarly, the relatively high intercepts of the dive duration-body mass relationships in ectotherms as compared to endotherms are consistent with well-established differences in the oxygen consumption rates of ectotherms and endotherms. On average, whole organism oxygen consumption rates of endothermic vertebrates are approximately 1–2 orders of magnitude higher than ectotherms after accounting for any effects of temperature (*Gillooly et al., 2001*; *Brown et al., 2004*). As such, endotherms would be expected to use their oxygen stores more quickly than ectotherms, and have dive durations roughly an order of magnitude lower than ectotherms-as was observed (Fig. 2).

Dive duration was also shown here to vary systematically with temperature (Table 1 and Fig. 2). Note that while temperature has been shown to affect the dive duration of individual species (*Priest & Franklin, 2002*; *Storch et al., 2005*), no broad-scale analyses of temperature on dive duration have been previously undertaken. The temperature dependence of the
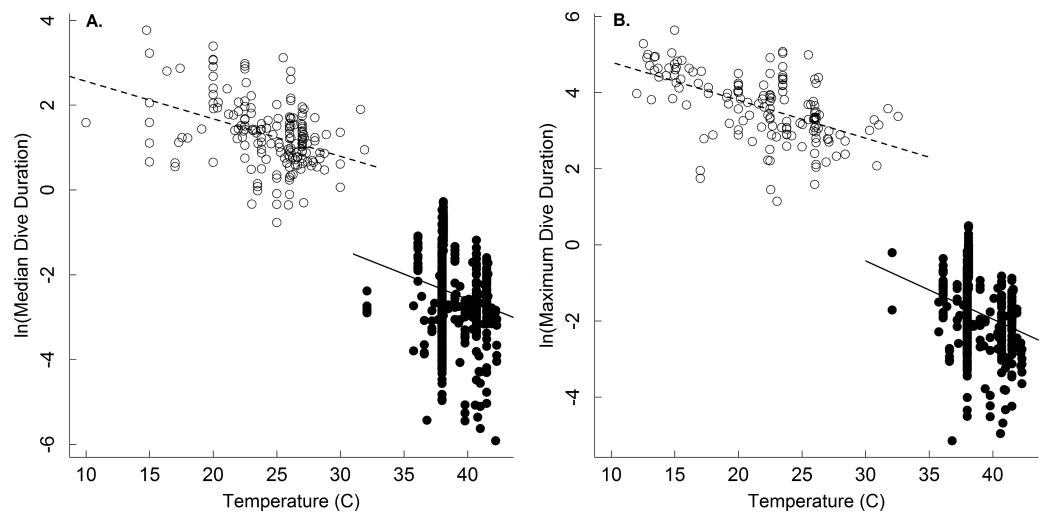
Figure 2 **The temperature dependence of dive duration in vertebrates.** The natural logarithm of body mass-corrected median (A) and maximum (B) dive duration as a function of temperature (°C) for endothermic (birds and mammals; closed points) and ectothermic vertebrates (reptiles and amphibians; open points, dashed line). Many species are represented by multiple points, as described in the methods (see Table 1 for statistics).

oxygen store/usage hypothesis described by Eq. (4) has not been fully appreciated since the hypothesis has largely been applied to endotherms. Our results show that, at least in ectotherms, median and maximum dive duration decreases with increasing temperature as $e^{-0.11}$ and $e^{-0.13}$, respectively (Table 1 and Fig. 2)-similar to that described by Eq. (4). This equates roughly to a Q_{10} of 2.5 such that dive duration will decrease by roughly 2.5-fold for every 10 °C increase in temperature. Thus, increases in environmental temperature could substantially reduce foraging time for ectothermic divers, and thus potentially affect individual fitness and population viability. The effect of any such increase would be most acute at warmer temperatures, where a smaller increase in temperature could have a greater effect on dive duration (see *Dillon, Wang & Huey, 2010*).

Together, these results point to the utility of the oxygen store/usage hypothesis for explaining some similarities and differences in dive duration among diverse vertebrates. Still, a deliberately simplified model such as this is perhaps most useful as a point of departure for examining species-specific adaptations for diving-both physiological and behavioral. Accounting for the effects of body mass and temperature on dive duration should be helpful in evaluating the benefit of such adaptations. More broadly, the model and results presented here demonstrate how considering the physiological effects of body size and temperature can reveal important insights into behavioral ecology (*Hayward, Gillooly & Kodric-Brown, 2012*).

ACKNOWLEDGEMENTS

ADDITIONAL INFORMATION AND DECLARATIONS

Competing Interests

The authors declare there are no competing interests.

Author Contributions

- April Hayward and James F. Gillooly conceived and designed the experiments, performed the experiments, analyzed the data, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.
- Mariela Pajuelo performed the experiments, analyzed the data.
- Catherine G. Haase analyzed the data, prepared figures and/or tables, reviewed drafts of the paper.
- David M. Anderson performed the experiments, analyzed the data, prepared figures and/or tables.

Data Availability

The following information was supplied regarding data availability:

The raw data has been supplied as a Supplementary File.

Supplemental Information

Supplemental information for this article can be found online at http://dx.doi.org/10.7717/peerj.2569#supplemental-information.

REFERENCES

Andrews RD, Enstipp MR. 2016. Diving physiology of seabirds and marine mammals: relevance, challenges and some solutions for field studies. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* In Press.

Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White J-SS. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution* 24:127–135 DOI 10.1016/j.tree.2008.10.008.

Bostrom BL, Jones DR. 2007. Exercise warms adult leatherback turtles. *Comparative Biochemistry & Physiology Part A: Molecular and Integrative Physiology* 147:323–331 DOI 10.1016/j.cbpa.2006.10.032.

Boyd IL. 1997. The behavioural and physiological ecology of diving. *Trends in Ecology & Evolution* 12:213–217 DOI 10.1016/S0169-5347(97)01054-9.

Brischoux F, Bonnet X, Cook TR, Shine R. 2008. Allometry of diving capacities: ectothermy vs. endothermy. *Journal of Evolutionary Biology* 21:324–329.

Brown JH, Gillooly JF, Allen AP, Savage VM, West GB. 2004. Response to Forum Commentary on ''Toward a Metabolic Theory of Ecology''. *Ecology* **85**:1818–1821 DOI 10.1890/03-0800.

Butler PJ, Jones DR. 1997. Physiology of diving of birds and mammals. *Physiological Reviews* **77**:837–899.

Butler PJ, Jones DR. 1982. The comparative physiology of diving in vertebrates. *Advances in Comparative Physiology and Biochemistry* **8**:179–364 DOI 10.1016/B978-0-12-011508-2.50012-5.

Campbell HA, Sullivan S, Read MA, Gordos MA, Franklin CE. 2010. Ecological and physiological determinants of dive duration in the freshwater crocodile. *Functional Ecology* **24**:103–111 DOI 10.1111/j.1365-2435.2009.01599.x.

Charnov E, Gillooly J. 2003. Thermal time: body size, food quality and the 10° C rule. *Evolutionary Ecology Research* **5**:43–51.

Clarke A, Rothery P. 2008. Scaling of body temperature in mammals and birds. *Functional Ecology* **22**:58–67 DOI 10.1111/j.1365-2435.2007.01341.x.

Dillon ME, Wang G, Huey RB. 2010. Global metabolic impacts of recent climate warming. *Nature* **467**:704–706 DOI 10.1038/nature09407.

Feder ME, Burggren WW. 1985. Cutaneous gas exchange in vertebrates: design, patterns, control and implications. *Biological Reviews* **60(1)**:1–45.

Frair W, Ackman RG, Mrosovsky N. 1972. Body temperature of *Dermochelys coriacea*: warm turtle from cold water. *Science* **177**:791–793 DOI 10.1126/science.177.4051.791.

Gillooly JF, Brown JH, West GB, Savage VM, Charnov EL. 2001. Effects of size and temperature on metabolic rate. *Science* **293**:2248–2251 DOI 10.1126/science.1061967.

Gillooly JF, Gomez JP, Mavrodiev EV, Rong Y, McLamore ES. 2016. Body mass scaling of passive oxygen diffusion in endotherms and ectotherms. *Proceedings of the National Academy of Sciences of the United States of America* **113**:5340–5345 DOI 10.1073/pnas.1519617113.

Hadfield JD. 2010. MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *Journal of Statistical Software* **33**:1–22 DOI 10.18637/jss.v033.i02c.

Halsey LG, Blackburn TM, Butler PJ. 2006. A comparative analysis of the diving behaviour of birds and mammals. *Functional Ecology* **20**:889–899 DOI 10.1111/j.1365-2435.2006.01170.x.

Halsey LG, Butler PJ, Blackburn TM. 2006. A phylogenetic analysis of the allometry of diving. *The American Naturalist* **167**:276–287 DOI 10.1086/499439.

Hayward A, Gillooly JF, Kodric-Brown AB. 2012. Behavior. In: Sibly RM, Brown JH, eds. *Metabolic ecology: a scaling approach.* Chicago: University of Chicago Press, 67–77.

Isaac NJ, Carbone C. 2010. Why are metabolic scaling exponents so controversial? Quantifying variance and testing hypotheses. *Ecology Letters* **13(6)**:728–735 DOI 10.1111/j.1461-0248.2010.01461.x.

Kembel SW, Cowan PD, Helmus MR, Cornwell WK, Morlon H, Ackerly DD, Blomberg SP, Webb CO. 2010. Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* **26**:1463–1464 DOI 10.1093/bioinformatics/btq166.

Kooyman GL. 1989. *Diverse divers: physiology and behavior.* Berlin: Springer-Verlag.

Kooyman GL, Ponganis PJ. 1998. The physiological basis of diving to depth: Birds and Mammals. *Annual Review of Physiology* **60**:19–32 DOI 10.1146/annurev.physiol.60.1.19.

Lenfant C, Johansen K. 1972. Gas exchange in gill, skin, and lung breathing. *Respiration Physiology* **14(1)**:211–218 DOI 10.1016/0034-5687(72)90029-1.

Lindstedt SL, Calder III WA. 1981. Body size, physiological time, and longevity of homeothermic animals. *The Quarterly Review of Biology* **56**:1–16.

Lunn DJ, Thomas A, Best N, Spiegelhalter D. 2000. WinBUGS-a Bayesian modelling framework: concepts, structure, and extensibility. *Statistics and Computing* **10**:325–337 DOI 10.1023/A:1008929526011.

Mirceta S, Signore AV, Burns JM, Cossins AR, Campbell KL, Berenbrink M. 2013. Evolution of mammalian diving capacity traced by myoglobin net surface charge. *Science* **340(6138)**:1234192 DOI 10.1126/science.1234192.

Nakagawa S, Schielzeth H. 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution* **4**:133–142 DOI 10.1111/j.2041-210x.2012.00261.x.

Paradis E, Claude J, Strimmer K. 2004. APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* **20**:289–290 DOI 10.1093/bioinformatics/btg412.

Penick DN, Spotila JR, O'Connor MP, Steyermark AC, George RH, Salice CJ, Paladino FV. 1998. Thermal independence of muscle tissue metabolism in the leatherback turtle, *Dermochelys coriacea. Comparative Biochemistry and Physiology—Part A: Molecular & Integrative Physiology* **120**:399–403 DOI 10.1016/S1095-6433(98)00024-5.

Priest TE, Franklin CE. 2002. Effect of water temperature and oxygen levels on the diving behavior of two freshwater turtles: *Rheodytes leukops* and *Emydura macquarii. Journal of Herpetology* **36(4)**:555–561.

Schreer JF, Kovacs KM. 1997. *Allometry of diving capacity in air-breathing vertebrates.* Ottawa: National Research Council of Canada.

Southwood AL, Andrews RD, Paladino FV, Jones DR. 2005. Effects of diving and swimming behavior on body temperatures of Pacific leatherback turtles in tropical seas. *Physiological and Biochemical Zoology* **78**:285–297 DOI 10.1086/427048.

Stephens PA, Carbone C, Boyd IL, McNamara JM, Harding KC, Houston AI. 2008. The scaling of diving time budgets: insights from an optimality approach. *The American Naturalist* **171**:305–314 DOI 10.1086/527491.

Storch S, Wilson RP, Hillis-Starr Z-M, Adelung D. 2005. Cold-blooded divers: temperature-dependent dive performance in the wild hawksbill turtle *Eretmochelys imbricata. Marine Ecology Progress Series* **293**:263–271 DOI 10.3354/meps293263.

White CR, Phillips NF, Seymour RS. 2006. The scaling and temperature dependence of vertebrate metabolism. *Biology Letters* **2**:125–127 DOI 10.1098/rsbl.2005.0378.