Common metabolic constraints on dive duration in endothermic and ectothermic vertebrates

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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.

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12 **Common Metabolic Constraints on Dive Duration in Endothermic**
13 **and Ectothermic Vertebrates**
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16 **Running Title:** Constraints on Vertebrate Dive Duration

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25   **Abstract**

26   Dive duration in air-breathing vertebrates is thought to be constrained by the volume of oxygen

27   stored in the body and the rate at which it is consumed (i.e., "oxygen store/usage hypothesis").

28   The body mass-dependence of dive duration among endothermic vertebrates is largely

29   supportive of this model, but previous analyses of ectothermic vertebrates show no such body

30   mass-dependence. Here we show that dive duration in both endotherms and ectotherms largely

31   support the oxygen store/usage hypothesis after accounting for the well-established effects of

32   temperature on oxygen consumption rates. Analyses of the body mass and temperature

33   dependence of dive duration in 181 species of endothermic vertebrates and 29 species of

34   ectothermic vertebrates show that dive duration increases as a power law with body mass, and

35   decreases exponentially with increasing temperature. Thus, in the case of ectothermic

36   vertebrates, changes in environmental temperature will likely impact the foraging ecology of

37   divers.

38   **Key Words:** diving behavior, metabolic theory, metabolism, thermal ecology, oxygen storage,

39   allometry, scaling

41 **Introduction**

42   The length of time that air-breathing vertebrate divers can remain submerged is an

43 important constraint on their foraging activities, and perhaps ultimately on their fitness (Butler &

44 Jones 1982; Kooyman 1989; Stephens et al. 2008; Andrews & Enstipp 2016). Consequently,

45 vertebrates display a wide variety of behavioral, morphological, and physiological adaptations to

46 enhance dive capacity. For example, endothermic vertebrates that dive show a relatively high

47 capacity to store oxygen, use anaerobic metabolism, and reduce oxygen demand in non-vital

48 tissues to prolong dive duration (Boyd 1997; Butler & Jones 1997; Kooyman & Ponganis 1998).

49 For example, with respect to oxygen storage, cetaceans have higher densities of myoglobin in

50 their tissues of a molecular form that has evolved to be more stable at depth (Mirceta et al. 2013).

51 Despite such specialization, maximum dive duration in endotherms varies somewhat predictably

52 with body mass based on the amount of oxygen stored in the body and the rate at which oxygen

53 is consumed (Butler & Jones 1982; Schreer et al. 1997; Halsey et al. 2006a; Halsey et al. 2006b;

54 Stephens et al. 2008). However, the extent to which dive duration may similarly vary with body

55 mass in ectotherms as predicted by the oxygen store/usage hypothesis is less clear. Recent

56 studies concluded that ectotherms fail to conform to expectations, and attributed this to

57 ectotherms possessing characteristics that weaken any allometric constraints associated with

58 diving (e.g., the ability to use aquatic respiration to supplement oxygen stores, and to enter

59 thermally-induced hypo-metabolic states, to extend dives) (Brischoux et al. 2008; Campbell et al.

60 2010). In the case of aquatic respiration, some air-breathers may respire in water using lungs,

61 whereas others may respire through their integument (i. e., "cutaneous respiration"; Lenfant &

62 Johansen 1972; Feder & Burggren 1985). Yet, the potentially confounding effects of temperature

63   on oxygen consumption rates and thus dive duration have not yet been examined in vertebrate

64   ectotherms.

65   Here we present broad-scale analyses of dive duration in both endothermic and

66   ectothermic vertebrates. We compare the predicted body mass and temperature dependence of

67   dive duration based on the oxygen store/usage hypothesis to analyses of extensive empirical data

68   compiled from the literature. The model and results presented here build on previous work in

69   endotherms (Butler & Jones 1982; Kooyman 1989; Stephens et al. 2008) to examine the

70   relationship in ectotherms, particularly with respect to temperature.

71   We begin by examining the predicted body mass and/or temperature dependence of dive

72   duration based on the oxygen store/usage hypothesis. This hypothesis stipulates that dive

73   duration (t_D) is a function of the total amount of oxygen carried by an organism on its dive (TO_2)

74   divided by the rate at which that oxygen is used (i.e. its metabolic rate, B) (Butler & Jones 1982;

75   Kooyman 1989). Thus,

76 $$t_D = TO_2 \, / \, B$$ [1]

77   where oxygen storage capacity scales approximately linearly with body mass (M) and is

78   independent of temperature (Lindstedt & Calder 1981; Stephens et al. 2008; Campbell et al.

79   2010) such that:

80 $$TO_2 = aM^1$$ [2]

81   , where a is a constant that describes the amount of oxygen that can be stored per gram of body

82   mass (Lindstedt & Calder 1981; Campbell et al. 2010). Oxygen consumption rate in Eq. 1,

83   however, has both a body mass and temperature dependence such that:

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$$B = c \bullet M^d \bullet e^{0.12\text{Tc}}$$
[3]

85 , where c is a constant describing the amount of oxygen consumed per unit body mass, d

86 describes the scaling of whole organism oxygen consumption rate with body mass (M), and

87 $e^{0.12\text{Tc}}$ describes the exponential temperature dependence of oxygen consumption rate that is

88 roughly equivalent to a Q_{10} of 2.5 (Charnov & Gillooly 2003). Thus, we expect that the oxygen

89 store/usage hypothesis should have both a body mass and temperature dependence such that:

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$$t_D = a \bullet c^{-1} \bullet M^{b-d} \bullet e^{-0.12\text{Tc}}$$
[4]

91 Note that the body mass dependence of oxygen consumption rate may differ between

92 endotherms and ectotherms (Gillooly et al. 2016), and thus the body mass dependence of dive

93 duration may also differ. Still, the scaling exponent for whole organism oxygen consumption rate

94 shown in Eq. 4 (i.e., "d") is expected to be close to a value of ¾ (Isaac & Carbone 2010) and thus

95 considerably less than the scaling exponent for oxygen storage (i.e., "b") of roughly 1. The effect

96 of temperature on oxygen consumption rate, though, appears to be more similar in both groups

97 (Gillooly et al. 2001). We evaluate the body mass and temperature dependence of dive duration

98 from Eq. 4 for a diverse assortment of mammals, birds, reptiles, and amphibians (Appendix 1).

99 **Methods**

100 *Data collection*

101 Data on median and maximum dive duration, body mass, and temperature were obtained

102 from previously published studies for 181 species of endotherms and 29 species of ectotherms

103 (Appendix 1). Leatherback turtles (*Dermochelys coriacea*) were excluded from consideration

104 since they are functionally endothermic (Penick et al. 1998; Southwood et al. 2005; Bostrom &

105   Jones 2007), and direct measures of body temperature were not available. The body temperature

106   of this species may be as much as 18°C higher than ambient temperatures (Frair et al. 1972).

107   For ectotherms, we used direct measuresof body temperature when available, but

108   otherwise we used ambient environmental temperatures as a proxy for body temperatures. For

109   endotherms, we used species-specific measures of body temperatures for mammals and birds

110   when available, or the mean body temperature of species from the same genus (Clarke & Rothery

111   2008). If both of these estimates were not available, we used the mean body temperatures of

112   birds (41.5 °C) and mammals (37 °C) (Clarke & Rothery 2008)(Appendix 1). For body mass, we

113   used the values of study subjects, or if unavailable, estimates of adult body masses from other

114   sources (Appendix 1).

115   *Analyses*

116   We evaluated the body mass and temperature dependence of median and maximum dive

117   duration using Bayesian generalized linear mixed-models (Lunn et al. 2000; Bolker et al. 2009)

118   implemented in R package *MCMCglmm* (Hadfield 2010). In performing these analyses, we

119   accounted for any non-independence due to shared evolutionary history by including a vertebrate

120   supertree recently constructed by (Gillooly et al. 2016), and by treating species as a random

121   effect. This approach also accounted for effects of species sample sizes. To evaluate statistical

122   models, we calculated conditional R^2 values for each model (Nakagawa & Schielzeth 2013), and

123   assessed model assumptions using diagnostic tests associated with phylogenetic analyses

124   (Paradis et al. 2004; Kembel et al. 2010).

125   To best assess the temperature-dependence of median and maximum dive duration, we

126   first performed analyses on the entire dataset. This dataset includes individuals of the same

127 species measured at different temperatures. To best assess the mass-dependence of dive duration,

128 we performed an additional set of analyses that was largely restricted to one point per species

129 except when body mass differed substantially between males or females of a species, or between

130 juveniles and adults. For this second set of analyses, median and maximum dive durations were

131 normalized to 30°C for all species by assuming a Q_{10} of 2.5 for oxygen consumption rate

132 (Gillooly et al. 2001; White et al. 2006).

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134 **Results and Discussion**

135   Results show support for the body mass and temperature dependence of dive duration

136 predicted by the oxygen store/usage hypothesis ((Butler & Jones 1982; Kooyman 1989); Eq. 4).

137 With respect to body mass, analysis of the full dataset showed that median and maximum dive

138 duration increased as a power law with body mass in both ectothermic and endothermic

139 vertebrates (Table 1). While scaling exponents varied from 0.09-0.42 depending on the group in

140 question, for ectotherms the 95 % confidence intervals of these scaling exponents included the

141 0.25 one would expect for dive duration (Table 1, Eq. 4) based on the linear scaling of oxygen

142 storage and a3/4 power scaling of oxygen consumption rate (Isaac & Carbone 2010; Gillooly et

143 al. 2016; but see White et al. 2006). In the case of endotherms, however, the confidence limits of

144 these analyses did not include ¾ (but did include 2/3; Table 1). Still, when the dataset was

145 restricted largely to one point per species, and adjusted to a common temperature, the scaling

146 exponents for median and maximum dive duration ranged from only 0.21 to 0.34, in closer

147 agreement with expectations from the oxygen store/usage hypothesis and the ¾ scaling of

148 oxygen consumption (Table 2; Eq. 4). With respect to ectotherms, then, our results differ from

149 previous studies showing no body mass dependence of dive duration (Brischoux et al. 2008;

150   Campbell et al. 2010). We speculate that this is because we explicitly accounted for the effects of

151   temperature.

152   A comparison of the body mass-dependence of dive duration in endothermic and

153   ectothermic vertebrates shows both similarities and differences-both of which are qualitatively

154   consistent with the oxygen store/usage hypothesis. First, body mass explained between 63-68 %

155   in temperature-adjusted median and maximum dive duration in both groups. However, the

156   scaling exponents for these relationships in ectotherms (0.21, 0.22) were slightly lower than

157   those of endotherms (0.31, 0.34; Figure 1, Table 2). This observation is consistent with work

158   showing that the body mass scaling of oxygen consumption rate is steeper in ectotherms

159   (exponents: 0.84-0.90) than in endotherms (0.70-0.74)(Gillooly et al. 2016). Similarly, the

160   relatively high intercepts of the dive duration-body mass relationships in ectotherms as compared

161   to endotherms are consistent with well-established differences in the oxygen consumption rates

162   of ectotherms and endotherms. On average, whole organism oxygen consumption rates of

163   endothermic vertebrates are approximately 1-2 orders of magnitude higher than ectotherms after

164   accounting for any effects of temperature (Gillooly et al. 2001; Brown et al. 2004). As such,

165   endotherms would be expected to use their oxygen stores more quickly than ectotherms, and

166   have dive durations roughly an order of magnitude lower than ectotherms-as was observed (Fig.

167   2).

168   Dive duration was also shown here to vary systematically with temperature (Table 1,

169   Figure 2) . Note that while temperature has been shown to affect the dive duration of individual

170   species (Priest & Franklin 2002; Storch et al. 2005) (, no broad-scale analyses of temperature on

171   dive duration have been previously undertaken. The temperature dependence of the oxygen

172   store/usage hypothesis described by Eq. 4 has not been fully appreciated since the hypothesis has

173   largely been applied to endotherms. Our results show that, at least in ectotherms, median and

174   maximum dive duration decreases with increasing temperature as $e^{-0.11}$ and $e^{-0.13}$, respectively

175   (Table 1, Figure 2)-similar to that described by Eq. 4. This equates roughly to a Q_{10} of 2.5 such

176   that dive duration will decrease by roughly 2.5-fold for every 10 °C increase in temperature.

177   Thus, increases in environmental temperature could substantially reduce foraging time for

178   ectothermic divers, and thus potentially affect individual fitness and population viability. The

179   effect of any such increase would be most acute at warmer temperatures, where a smaller

180   increase in temperature could have a greater effect on dive duration (see Dillon et al. 2010).

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182   Together, these results point to the utility of the oxygen store/usage hypothesis for

183   explaining some similarities and differences in dive duration among diverse vertebrates. Still, a

184   deliberately simplified model such as this is perhaps most useful as a point of departure for

185   examining species-specific adaptations for diving-both physiological and behavioral. Accounting

186   for the effect of body mass and temperature on dive duration should be helpful in evaluating the

187   benefit of such adaptations. More broadly, the model and results presented here demonstrate how

188   considering the physiological effects of body size and temperature can reveal important insights

189   into behavioral ecology (Hayward, Gillooly, & Kodric-Brown 2012).

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194 **Table 1: Body mass and temperature dependence of dive duration in vertebrates.** Outputs

195 from generalized linear mixed-models relating dive duration (median or maximum, in minutes)

196 to body mass (natural log-transformed, in grams) and temperature (°C). Conditional R^2 values

197 are reported, along with the slopes and intercepts of the relationships, and the sample sizes (N;

198 with number of species). Results shown here represent the full dataset with multiple individuals

199 for many species.

Model	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	1005 (210)
	Max.	3.34 (1.98,4.56)	0.32 (0.27,0.38)	-0.12 (-0.14,-0.10)	0.28	1005 (210)

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209 **Table 2: Body mass dependence of temperature-adjusted dive duration in vertebrates.**

210 Outputs from generalized linear mixed-models relating temperature-adjusted dive duration

211 (median or maximum) to body mass (ln-transformed, in grams) for ectothermic (amphibians and

212 reptiles) and endothermic (mammals and birds) vertebrates. Conditional R^2 values are reported,

213 along with the slopes and intercepts of the relationships, and sample sizes (N; with number of

214 species).

Model	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)

215

216 **Figure 1: The body mass dependence of dive duration in vertebrates.** The natural logarithm

217 of median (left) and maximum dive duration (min.; right) as a function of the natural logarithm

218 of body mass (g) for air-breathing endothermic (birds and mammals; closed points, solid line)

219 and ectothermic vertebrates (reptiles and amphibians; open points, dashed line). Data were

220 normalized to 30 °C assuming a Q_{10} of 2.5. Most points represent a single species (see Methods,

221 and Table 2 for statistics).

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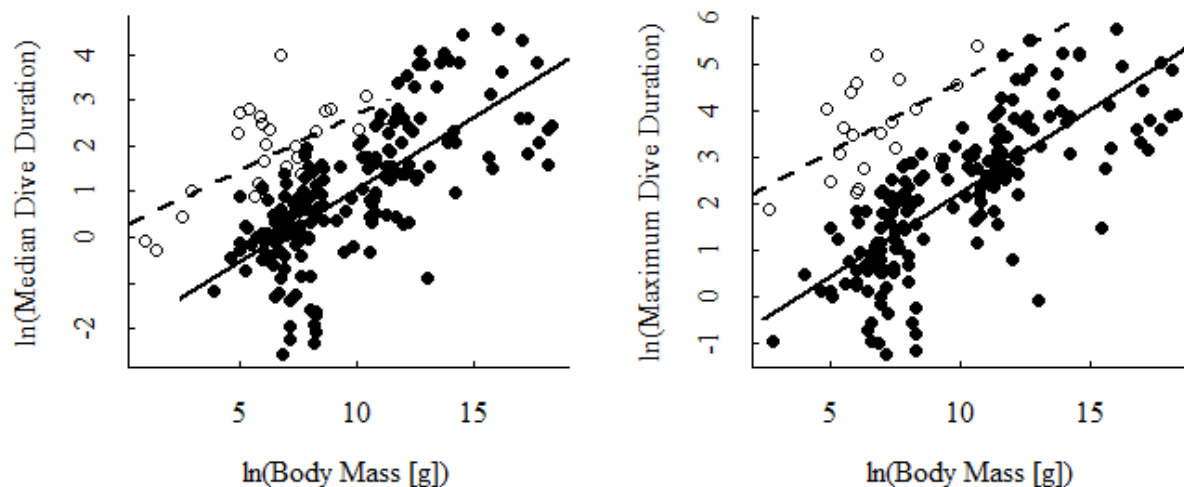
228 **Figure 2: The temperature dependence of dive duration in vertebrates.** The natural

229 logarithm of body mass-corrected median (left) and maximum (right) dive duration as a function

230 of temperature (ºC) for endothermic (birds and mammals; closed points) and ectothermic

231 vertebrates (reptiles and amphibians; open points, dashed line). Many species are represented by

232 multiple points, as described in the methods (see Table 1 for statistics).

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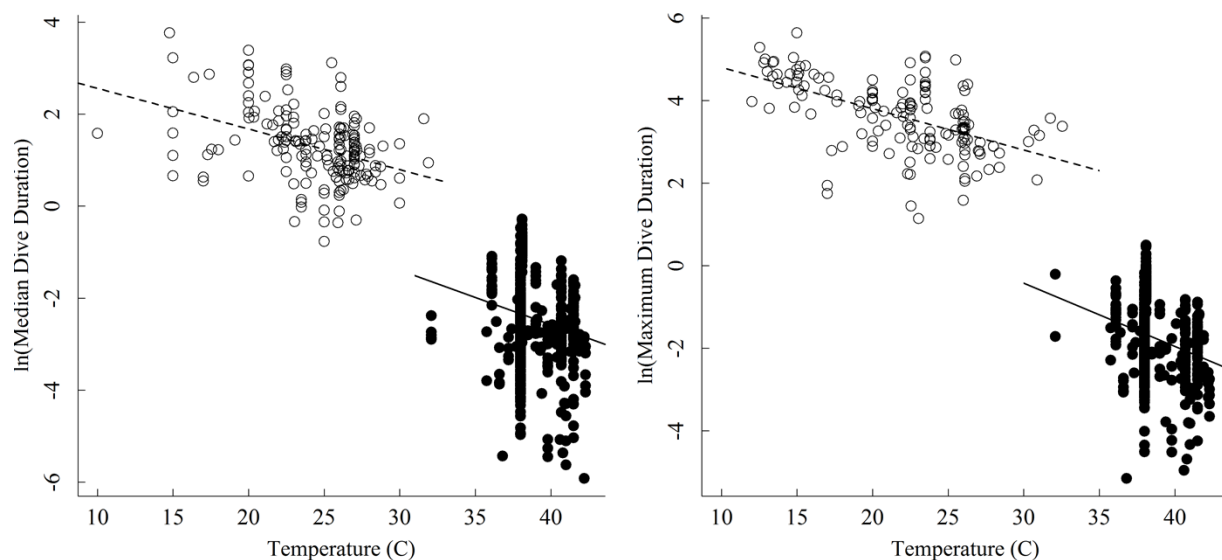
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245

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