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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

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Introduction

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

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

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

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

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

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

55   ectotherms possessing characteristics that weaken any allometric constraints associated with

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

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

58   2010). Yet, the potentially confounding effects of temperature on oxygen consumption rates and

59   thus dive duration have not yet been examined in vertebrate ectotherms.

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

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

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

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

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

65   relationship in ectotherms, particularly with respect to temperature.

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

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

68   duration (t_D) is a function of the total amount of oxygen carried by an organisms on its dive

69   (TO_2) divided by the rate at which that oxygen is used (i.e. its metabolic rate, B) (Butler & Jones

70   1982; Kooyman 1989). Thus,

71                                  $$t_D = TO_2 \, / \, B \qquad\qquad [1]$$

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

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

74   2010) such that:

75                                  $$TO_2 = aM^1 \qquad\qquad [2]$$

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

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

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

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

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

81   describes the scaling of oxygen consumption rate with body mass (M), and $e^{0.12Tc}$ describes the

82   exponential temperature dependence of oxygen consumption rate that is roughly equivalent to a

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83   Q_{10} of 2.5 (Charnov & Gillooly 2003). Thus, we expect that the oxygen store/usage hypothesis

84   should have both a body mass and temperature dependence such that:

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

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

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

88   duration may also differ. The effect of temperature on oxygen consumption rate, though, appears

89   to be more similar in both groups (Gillooly et al. 2001). We evaluate the body mass and

90   temperature dependence of dive duration from Eq. 4 for a diverse assortment of mammals, birds,

91   reptiles, and amphibians (Appendix 1).

92   **Methods**

93   *Data collection*

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

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

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

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

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

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

100   For ectotherms, we used direct estimates of body temperature when available, but

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

102   endotherms, we used species-specific estimates of body temperatures for mammals and birds

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

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104 2008). If both of these estimates were not available, we used the mean body temperatures of

105 birds (41.5 $^{\circ}$C) and mammals (37 $^{\circ}$C) (Clarke & Rothery 2008)(Appendix 1). For body mass, we

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

107 sources (Appendix 1).

108 *Analyses*

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

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

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

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

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

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

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

116 assessed model assumptions using diagnostic tests associated with phylogenetic analyses

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

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

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

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

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

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

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

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

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

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Results and Discussion

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

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

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

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

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

133   question, the 95 % confidence intervals of these scaling exponents included the 0.25-0.33 value

134   one would expect or dive duration (Table 1, Eq. 4) based on the linear scaling of oxygen storage

135   and the 2/3-3/4 power scaling of oxygen consumption rate(White et al. 2006; Gillooly et al.

136   2016). Moreover, when the dataset was restricted largely to one point per species, and adjusted to

137   a common temperature, the scaling exponents for median and maximum dive duration ranged

138   from only 0.21 to 0.31, in closer agreement with expectations from the oxygen store/usage

139   hypothesis (Table 2; Eq. 4). With respect to ectotherms, then, our results differ from previous

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

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

142   temperature.

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

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

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

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

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

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

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

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

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

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

153   of ectotherms and endotherms. On average, the oxygen consumption rates of endothermic

154   vertebrates are approximately 1-2 orders of magnitude higher than ectotherms (Gillooly et al.

155   2001; Brown et al. 2004). As such, endotherms would be expected to use their oxygen stores

156   more quickly than ectotherms, and have dive durations roughly an order of magnitude lower than

157   ectotherms-as was observed (Fig. 2).

158   Still, perhaps more surprising here is the observation that dive duration varies

159   systematically with temperature. Note that while temperature has previously been shown to

160   affect the dive duration of individual species (Storch et al. 2005) (Priest & Franklin 2002), no

161   broad-scale analysis of temperature on dive duration have been previously undertaken. The

162   temperature dependence of the oxygen store/usage hypothesis described by Eq. 4 has not been

163   fully appreciated since the hypothesis has largely been applied to endotherms. Our results show

164   that, at least in ectotherms, median and maximum dive duration decreases with increasing

165   temperature as $e^{-0.11}$ and $e^{-0.13}$, respectively (Table 1, Figure 2)-similar to that described by Eq. 4.

166   This equates roughly to a Q_{10} of 2.5 such that dive duration will decrease by roughly 2.5-fold for

167   every 10 $^{\circ}$C increase in temperature. Thus, increases in environmental temperature could

168   substantially reduce foraging time for ectothermic divers, and thus potentially affect individual

169   fitness and population viability. The effect of any such increase would be most acute at warmer

170   temperatures, where a smaller increase in temperature could have a greater effect on dive

171   duration (see Dillon et al. 2010).

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

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

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

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

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

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

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

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

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

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

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

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

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

198   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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213 **Table 2: Body mass dependence of temperature-adjusted dive duration in vertebrates.**

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

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

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

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

218 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)

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

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

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

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

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

225   and Table 2 for statistics).

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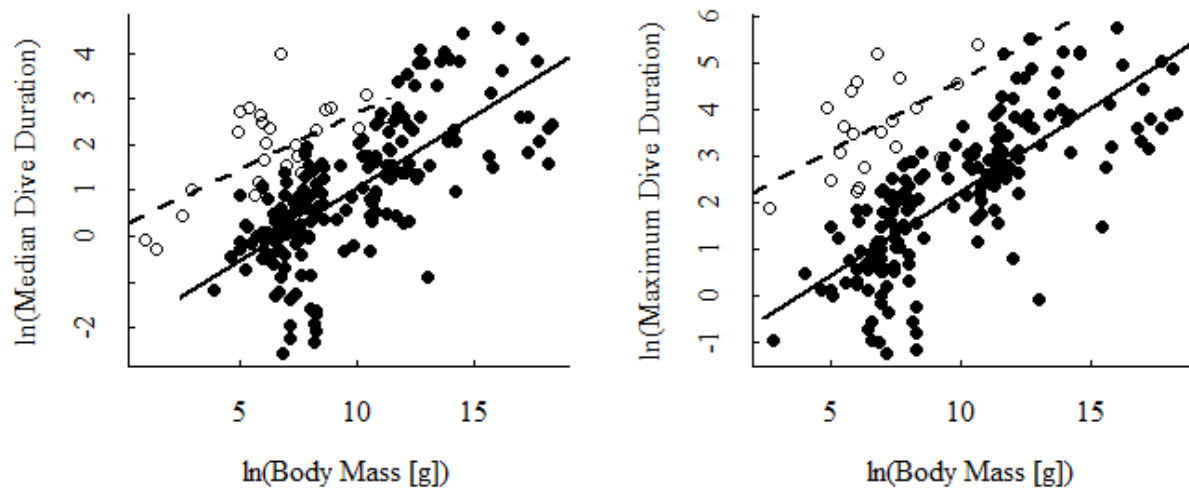
232 **Figure 2: The temperature dependence of dive duration in vertebrates.** The natural

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

234 of temperature (°C) for endothermic (birds and mammals; closed points) and ectothermic

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

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

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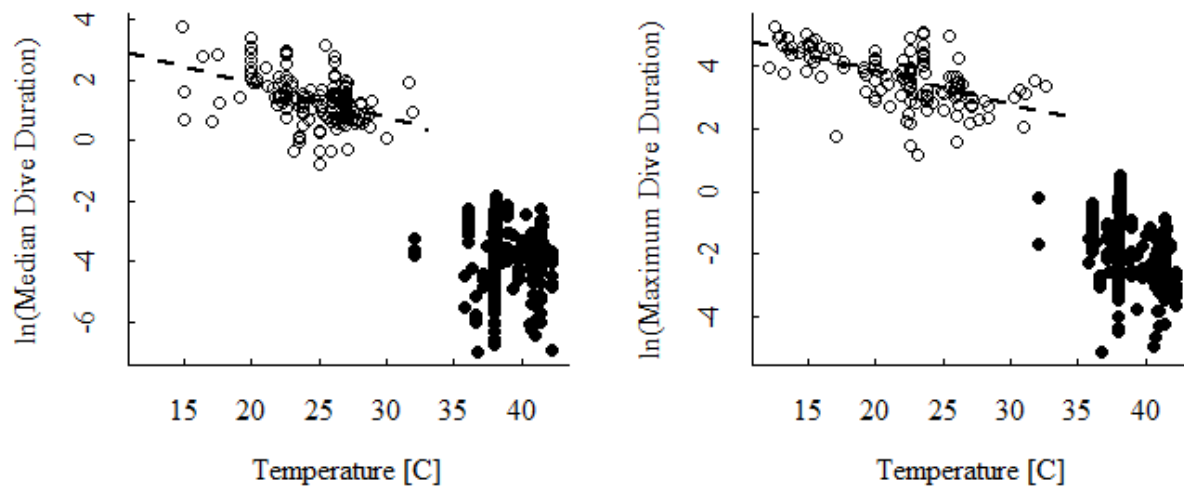
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